Abstract—Larval and early juvenile stages of Symphurus oligomerus are described from 24 specimens from the Gulf of California. Meristic features were 48-49 total vertebrae, 87-94 dorsal-fin rays, 73-77 anal-fin rays, 12 caudal-fin rays, and five hypural bones. Seven larvae and one juvenile were cleared and stained to obtain the pterygiophore formula (1-3-2-2-2) that confirmed the identification of S. oligomerus. The pigment pattern from preflexion to juvenile stage consists of three bands on the dorsal margin and two bands on the ventral margin formed by star-shaped melanophores on the left side of the body. The intestine in preflexion to postflexion larvae forms an abdominal projection that ends in a short conical appendix. The intestine is supported by three cartilaginous struts; larvae with these physical attributes are called exterilium larvae. Preflexion larvae have two elongated dorsal-fin rays, and in flexion to postflexion larvae the second to the fourth dorsalfin rays are elongate. We found an apparent connection between the size at metamorphosis of the species of Symphurus and the depth distribution range of adults such that the fish species that metamorphose at a larger size have a deeper distribution as adults and exterilium larvae seem to correspond to species that have deeper distributions.

Manuscript submitted 15 October 2008. Manuscript accepted 20 October 2009. Fish. Bull. 108:45–55 (2010).

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Larval development of the spotfin tonguefish (*Symphurus oligomerus* Mahadeva and Munroe, 1990) (Pleuronectiformes: Cynoglossidae) from the Gulf of California, Mexico

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The Cynoglossidae family in the eastern Pacific Ocean is represented by a single subfamily (Symphurinae) and a single genus (Symphurus; tonguefish). This genus has a world-wide distribution, including the eastern Pacific Ocean where it is represented by 18 species, inhabiting temperate and tropical waters on the continental shelf and slope (Munroe et al., 1995: Munroe and Robertson, 2005). Previous studies have demonstrated the diagnostic value of the pterygiophore interdigitation pattern (ID pattern) which, combined with other meristics, can be used to identify symphurine tonguefish all over the world (Munroe, 1992; Munroe et al., 1995). Species with the 1-3-2 and 1-3-3 ID patterns are found in both the Atlantic Ocean and in the tropical eastern Pacific Ocean from the Gulf of California to northern Peru. Species with the 1-3-4, 1-4-2, 1-4-3 and 1-5-3 ID patterns are found only in the New World. Currently, the early life history stages of seven species of symphurine tonguefishes occurring in the eastern Pacific can be distinguished from each other by their melanistic pigmentation patterns. Symphurus callopterus has an accumulation of pigment in the form of two oblique, incomplete and two complete bands on the caudal

section of the body (Evseenko, 1990), whereas S. williamsi (Aceves et al., 1999), S. elongatus (Charter and Moser, 1996), S. chabanaudi, and S. prolatinaris (Evseenko and Shtaut, 2000) have blotches or spots or both on the dorsal and ventral margins of the body; and both S. atricaudus (Charter and Moser, 1996) and S. atramentatus (Saldierna-Martínez et al., 2005) have a series of dash-like spots on the dorsal and ventral margins of the body. Although S. oligomerus (spotfin tonguefish) is a species with wide distribution from the Gulf of California to Panama (Mahadeva and Munroe. 1990; Munroe et al., 1995), its larvae are still undescribed. This study provides the first description of the larval development of S. oligomerus from the preflexion to the juvenile stage.

Materials and methods

Plankton samples were collected in November 2005 in the Gulf of California. Twenty-four oblique zooplankton tows were made with bongo nets with a mouth diameter of 60 cm and net mesh of 505 and 333 μ m as detailed in Kramer et al. (1972). Three additional samples were obtained from multilevel oblique tows at 150–100, 100–50, and

Table 1Sampling methods, locations, depths, and preservation methods for larval *Symphurus oligomerus* collected in the Gulf of California in 2005. B=bongo net, M=multilevel net, BL=body length.

	Coordi	inates	Number of specimens (BL, mm)						
Net	N	W	Catch depth (m)	Ethyl alcohol	Formalin				
В	28°30′38″	113°6′39″	0-21	1 (18.0)					
В	$28^{\circ}12'$	$112^{\circ}17'$	0-195	1 (15.8)					
В	$27^{\circ}28'46''$	$112^{\circ}16'27''$	0-214		1 (18.2)				
В	$27^{\circ}14'24''$	111°14′24″	0-211	1 (14.6)					
В	$26^{\circ}54'30''$	111°46′16″	0-71		2(3.0-3.4)				
В	$26^{\circ}36'1.5''$	$110^{\circ}32'1.5''$	0-209	1 (8.8)	3 (3.8–18.0)				
В	26°11′19″	111°18′31″	0-182		3(1.6-2.6)				
В	$25^{\circ}24'40''$	109°16′28″	0-45	5 (6.8–10.4)					
В	$24^{\circ}52'26''$	109°48′19″	0-97	1 (12.0)					
M	$24^{\circ}42'8''$	110°17′28″	0-50		1 (10.0)				
M	$24^{\circ}42'8''$	110°17′28″	50-100		2 (11.3–12.3)				
M	24°42′8″	110°17′28″	100-150		2(7.8-10.4)				

50-0 m with simple conical nets with a mouth diameter of 75 cm and net mesh of 333 μ m (Table 1). Samples obtained with the 333- μ m mesh bongo net and the multilevel tows were fixed in ethyl alcohol (96%), and samples from the $505-\mu$ m mesh bongo net were fixed with 10% formalin solution buffered with sodium borate.

Among the fish larvae taken in this collection, twenty-four specimens of larval and juvenile Symphurus (1.6–18.2 mm body length [BL]) were grouped because they shared the same meristic counts and pigmentation patterns. Comparison of this group of larvae with published descriptions of the early life stages of tonguefish from the eastern Pacific (Evseenko, 1990; Charter and Moser, 1996; Aceves et al., 1999; Evseenko and Shtaut, 2000; and Saldierna-Martínez et al., 2005) indicated that these specimens belonged to a species whose larval development had not been described. Seven larvae and one juvenile from this group of specimens were cleared and stained (Potthoff, 1984) and identified as Symphurus oligomerus on the basis of meristic characters (dorsal-fin rays, anal-fin rays, caudal-fin rays, total vertebrae, and hypural bones) and interdigitation of dorsal-fin pterygiophores and neural spines (ID pattern), which was 1-3-2-2 (Mahadeva and Munroe, 1990; Munroe, 1992; Munroe et al., 1995). Subsequently a developmental series of larvae was assembled by using similar pigmentation pattern (oblique band on the body) as well as meristic and morphometric features (total dorsal and anal-fin rays and conical appendix). Measurements to the nearest 0.1 mm were taken on the left side of the body as illustrated in Figure 1C and Table 2 by using a stereomicroscope (Stemi 2000-C, Zeiss) fitted with an ocular micrometer.

All larvae and juveniles were deposited in the Colección científica de huevos y larvas de peces del Pacífico Mexicano (ICTIOPLANCTON) registered with the Secretaría del Medio Ambiente y Recursos Naturales (B.C.S.-INV196-06-07) and located at the Departamento de Plancton y Ecología Marina, Centro Interdisciplinario de Ciencias Marinas-Instituto Politécnico Nacional (CICIMAR-IPN). Catalogue numbers for specimens of *S. oligomerus* deposited in this collection are L108–L126.

Illustrations of larval and juvenile stages of *S. oligomerus* were drawn with a camera lucida (Stereomicroscope Stemi SV8, Zeiss). Descriptions of larval and juvenile stages were based on 24 specimens from 1.6 to 18.2 mm BL. None of the specimens were in the yolksac stage, indicating that hatching takes place at sizes <1.6 mm notochord length (NL). Preflexion, flexion, postflexion, and juvenile stages accord with the larval fish developmental stages described by Ahlstrom (1976).

Results

Identification

Twenty-four specimens sharing similar morphometric and meristic characteristics were identified among the material examined. Seven larvae and one juvenile tonguefish from 7.8–18.2 mm BL were cleared and stained. These cleared specimens had the following ID patterns: 1-3-2-2-2 (n=7) and 2-3-2-2-2 (n=1). We observed differences in the number of hypural elements in the cleared and stained specimens; these differences were associated with the development stage, as well as with the degree of ossification of the hypural elements. Five hypural bones were observed in one postflexion larva and one juvenile (18.0 and 18.2 mm BL); four cartilaginous hypurals were present in four larvae (10.4 to 12.0 mm BL), and three cartilaginous hypurals were present in two larvae (7.8 and 10.0 mm BL). From these

Table 2

Abbreviations and definitions of terms used to describe the morphometric and meristic characters of *Symphurus oligomerus* larvae and juveniles.

Body length (BL)	In preflexion and flexion stages, horizontal distance from snout tip to tip of notochord, referred to as notochord length (NL); in postflexion-stage larvae, from snout tip to posterior margin of hypural bones as standard length (SL) $ \frac{1}{2} \left(\frac{1}{2} \right) = \frac{1}{2} \left(\frac{1}{2} \right) $
Caudal region length (CRL)	Horizontal distance from posterior end of anus to tip of notochord in young larvae or to posterior margin of hypural bones in more developed larvae
Snout-anus length (SAL)	Horizontal distance through midline of body from snout tip to posterior margin of anus
Head length (HL)	Horizontal distance through midline of the head from snout tip to margin of cleithrum preceding pectoral fin base in small specimens, or to posterior margin of opercle in larger specimens
Eye diameter (ED)	Horizontal distance between anterior and posterior margins of left eye
Body depth at pelvic fin base (BD)	Vertical distance from dorsal to ventral margin of body, measured at pelvic fin base
Body depth at anus (BDA)	Vertical distance across body at anus prior to formation of dorsal fin pterygiophores (Moser, 1996)
Loop intestinal length (LIL)	Horizontal distance from cleithrum to tip of the conical appendix on the abdominal projection $% \left(1\right) =\left(1\right) \left(1\right) \left$
Abdominal projection length (APL)	Horizontal distance from cleithrum to base of conical appendix on abdominal projection
Conical appendix length (CAL)	Horizontal distance from base to tip of conical appendix
Pterygiophore interdigitation pattern (ID pattern)	Number of proximal dorsal-fin pterygiophores in each of the five anterior interneural spaces (Munroe, 1992).
Internal cartilaginous struts (ICS)	Support internal of the intestinal sac, make-up for cartilaginous struts

specimens and the remaining 14 larvae and two juveniles, we counted 48-49 vertebrae (more frequently 48), 87–94 dorsal-fin rays (more frequently 89–91), 73–77 anal-fin rays (more frequently 74–75), and 12 caudal-fin rays (Table 3). Of 18 species of Symphurus recognized in the eastern Pacific, only S. gorgonae, S. oligomerus, S. microlepis, and S. diabolicus have the 1-3-2-2-2 ID pattern. Symphurus gorgonae differs from the other species in having only four hypural bones, and S. oligomerus, S. microlepis, and S. diabolicus have five hypural bones (Munroe, 1992). Symphurus diabolicus and S. microlepis have more dorsal- (106-110 and 106, respectively) and anal- (89-96 and 92) fin rays and a higher number of vertebrae (57-59 and 57) than S. oligomerus (87-97 dorsal-fin rays, 72–83 anal-fin rays, and 48–52 total vertebrae). *Symphurus gorgonae* has fewer dorsal- (80–89) and anal- (63–74) fin rays than S. oligomerus (Munroe, 1992; Munroe and McCosker, 2001). Furthermore, S. diabolicus, is apparently endemic to the Galapagos Archipelago (Munroe and McCosker, 2001), whereas S. microlepis is collected off the coast of Panama in 530 m (Munroe et al., 1995; Munroe and McCosker, 2001). The combination of meristic features indicates that these larvae and juvenile specimens are S. oligomerus.

Description of larval and juvenile stage of *Symphurus oligomerus*

Morphological features The early preflexion larvae (1.6) and 2.6 mm BL) have an elongate, slightly compressed body. The abdominal cavity with an intestinal loop extends beyond the lower contour of the body, forming a short and freely hanging abdominal projection. This projection is an elongate and relatively slender sac with transparent walls; the loop intestinal length ranges between 21% and 31% of the BL (Table 4). The end portion of the abdominal projection is a conical appendix whose length is 2.5-10% of the BL. During flexion until the juvenile stage (7.8-18.2 mm BL) the loop of the intestine is supported by three internal cartilaginous struts (ICS); two are located on either side of the intestinal sac (Figs. 1C and 2A) and the third is located near the pectoral fin base, supporting the lateral cartilages. The anus opens on the left side of the body. The head is small, 25% of BL (Table 4) and has a small and oblique snout. The posterior corner of the mouth never extends beyond the middle part of the left eye (Fig. 1A). In larvae between 3.4 mm BL and 3.8 mm BL, the swim bladder is located above the dorsal region of the intestinal sac

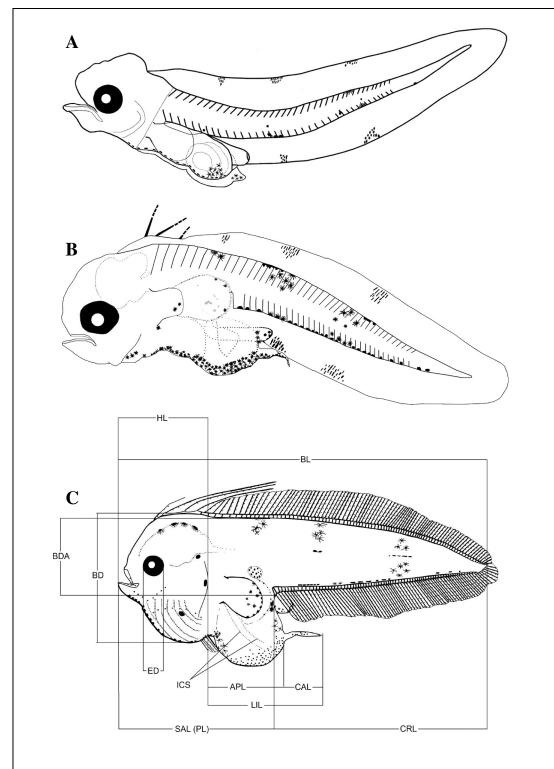


Figure 1

Spotfin tonguefish (Symphurus oligomerus): (A) preflexion larva (2.5 mm notochord length, NL); (B) preflexion larva (3.4 mm NL); and (C) flexion larva (7.8 mm body length) showing two internal cartilaginous struts (ICS). Morphometric measurements are HL=head length; BL=body length; CRL=caudal region length; SAL=snout—anus length; LIL=loop intestinal length; APL=abdominal projection length; CAL=conical appendix length; ED=eye diameter; BD=body depth at pelvic fin base; BDA=body depth at anus. Drawings by R. Saldierna.

						Tal	Table 3									
Larval and juvenile measurements (mm) for 24 specimens of spotfin tonguefish (Symphurus oligomerus) at various developmental stages: body length (BL), eye diameter (ED), head length (HL), snout—anus length (SAL), caudal region length (CRL), body depth at pelvic fin base (BD), body depth at anal fin (BDA), loop intestinal length (LLL), abdominal projection length (APL), conical appendix length (CAL), dorsal rays (DR), anal rays (AR), caudal rays (CR), total vertebrae (TV), hypural bones (H), and pterygiophore interdigitation pattern (ID). Not determined (nd) and incomplete dorsal-, and caudal-fin rays (+).	nents (mi t–anus le ength (Al tion patte	m) for 24 ingth (SA PL), conic ern (ID).	specimen NL), caud: sal appen Not deter	is of spoti al region dix lengt	fin tongur length (1 j.h (CAL), nd) and ir	efish (Sy. CRL), bo dorsal r	mphuru: dy deptl ays (DR e dorsal·	oecimens of spotfin tonguefish (Symphurus oligomerus) at various develop, caudal region length (CRL), body depth at pelvic fin base (BD), body (I appendix length (CAL), dorsal rays (DR), anal rays (AR), caudal rays of determined (nd) and incomplete dorsal-, anal-, and caudal-fin rays (+)	rus) at va c fin basa ys (AR), nd cauda	arious de e (BD), b caudal r al-fin ray	velopmer ody dept ays (CR) s (+).	ntal stag h at ana), total v	es: body l fin (BD ertebrae	length (A), loop (TV), h	BL), eye intesti ypural	oecimens of spotfin tonguefish (Symphurus oligomerus) at various developmental stages: body length (BL), eye diameter b), caudal region length (CRL), body depth at pelvic fin base (BD), body depth at anal fin (BDA), loop intestinal length 1 appendix length (CAL), dorsal rays (DR), anal rays (AR), caudal rays (CR), total vertebrae (TV), hypural bones (H), of determined (nd) and incomplete dorsal-, anal-, and caudal-fin rays (+).
								Measurement	ement							
Development stage	BL	ED	HI	SAL	CRL	BD	BDA	LIL	APL	CAL	DR	AR	$_{ m CR}$	TV	Н	ID
Start of preflexion	1.6	0.10	0.3	8.0	8.0	0.3	0.1	0.49	0.5	0.04						
	2.5	0.19	0.5	6.0	1.6	0.4	0.2	0.60	0.5	0.1						
	2.6	0.19	9.0	1.0	1.7	0.5	0.2	0.71	9.0	0.1						
	3.0	0.20	9.0	1.2	1.8	0.7	0.3	99.0	0.5	0.1						
	3.4	0.27	8.0	1.3	2.1	8.0	0.4	1.01	0.7	0.3						
	3.8	0.29	6.0	1.3	2.4	1.0	0.5	96.0	9.0	0.4						
	8.9	0.32	1.7	2.6	4.2	2.0	1.3	1.60	1.1	0.5	+08	404				
	7.0	0.40	1.6	2.7	4.2	2.1	1.3	1.92	1.4	0.5	+08	70+	2+			
Start of flexion	7.1	0.36	1.2	2.7	4.4	2.3	1.4	1.62	1.0	9.0	84+	70+	+9			
	7.4	0.40	2.3	3.0	4.4	2.4	1.3	pu	1.4	pu	06	74	+9			
	7.8	0.40	2.2	3.1	4.7	2.7	1.4	2.26	1.5	8.0	91	75	+9	48	က	1-3-2-2-2
	8.8	0.40	2.1	3.0	5.8	2.1	1.8	pu	pu	pu	pu	pu	12			
	10.0	0.46	2.5	3.9	6.1	3.3	2.0	3.45	2.2	1.3	91	75	12	49	က	2-3-2-2-2
	10.4	0.46	2.8	4.1	6.2	3.3	2.0	3.45	2.3	1.2	87	74	12	48	4	1-3-2-2-2
	10.4	0.48	2.7	3.8	9.9	3.4	2.2	3.14	2.2	1.0	+08	74	12			
	10.6	0.46	2.8	4.1	6.4	3.3	2.2	2.99	1.8	1.2	91	74	12	49	4	1-3-2-2-2
	11.3	0.46	3.1	4.6	6.7	3.7	2.2	3.91	2.5	1.4	06	74	12	48	4	1-3-2-2-2
	12.0	0.46	3.0	4.6	7.4	3.5	2.3	3.44	5.6	6.0	88	73	12			
	12.3	0.46	3.0	4.6	7.7	4.0	8.7	2.99	1.8	1.2	68	75	12	49	4	1-3-2-2-2
	14.6	0.48	3.7	5.8	8.9	4.3	3.1	3.58	2.5	1.1	94	75	12			
Start of postflexion	18.0	0.58	4.5	6.3	11.7	4.9	3.3	4.37	3.5	6.0	68	75	12	48	ည	1-3-2-2-2
Start of juvenile	15.8	09.0	3.5	5.2	10.6	3.8	3.2	2.51	1.8	0.7	88	27	12			
	18.0	0.58	3.5	4.9	13.1	4.0	3.7				06	22	12			
	18.2	0.69	5.1	6.1	12.1	4.0	3.0				88	92	12	48	ಸ	1-3-2-2-2

Table 4

Morphometric proportions of larval and juvenile spotfin tonguefish (*Symphurus oligomerus*) by percentage of body length (BL, mm): eye diameter (ED), head length (HL), caudal region length (CRL), snout—anus length (SAL), body depth at pelvic fin base (BD), body depth at anal fin (BDA), loop intestinal length (LIL), abdominal projection length (APL), conical appendix length (CAL). nd = not determined.

					% o	f BL										
Development stage	BL(mm)	ED	HL	CRL	SAL	BD	BDA	LIL	APL	CAL						
Start of preflexion	1.6	6.09	21.79	51.15	48.72	18.27	7.31	31.67	29.23	2.44						
	2.5	7.55	18.67	64.15	35.85	16.98	8.49	23.58	18.87	4.72						
	2.6	7.28	21.84	63.22	36.78	17.24	8.39	27.36	21.84	5.52						
	3.0	6.41	19.24	59.01	41.05	21.81	10.26	21.81	17.96	3.85						
	3.4	8.04	22.86	61.43	38.57	22.86	11.43	30.00	20.00	10.00						
	3.8	7.59	22.78	64.56	35.34	25.32	12.66	25.32	15.19	10.13						
	6.8	4.71	24.71	62.35	38.82	29.41	18.82	23.53	16.47	7.06						
	7.0	5.75	22.99	59.77	39.08	29.89	18.39	27.59	20.69	6.90						
Start of flexion	7.1	5.04	16.53	62.18	37.82	32.77	20.17	22.69	14.29	8.40						
	7.4	5.38	31.18	59.14	40.86	32.26	17.20	nd	19.35	nd						
	7.8	5.10	27.55	60.20	39.80	34.69	18.37	28.78	18.98	9.80						
	8.8	4.55	23.64	65.45	34.55	23.64	20.00	nd	nd	nd						
	10.0	4.60	25.29	60.92	39.08	33.33	19.54	34.43	21.79	12.64						
	10.4	4.44	26.67	60.00	40.00	32.22	19.44	33.33	22.22	11.11						
	10.4	4.59	25.69	63.30	36.70	33.03	21.10	30.28	21.10	9.17						
	10.6	4.35	26.09	60.87	39.13	31.52	20.65	28.26	17.39	10.87						
	11.3	4.08	27.55	59.18	40.82	32.65	19.39	34.69	22.45	12.24						
	12.0	3.85	25.00	61.54	38.46	28.85	19.23	28.76	21.40	7.36						
	12.3	3.74	24.30	62.62	37.38	32.71	22.43	24.30	14.95	9.35						
	14.6	3.29	25.20	60.66	39.37	29.13	21.26	24.53	17.32	7.21						
Start of postflexion	18.0	3.19	24.88	65.06	35.08	27.43	18.50	24.24	19.13	5.10						
Start of juvenile	15.8	3.81	21.90	67.15	32.85	24.09	20.44	15.93	11.68	4.25						
	18.0	3.20	19.22	73.04	27.55	22.42	20.50									
	18.2	3.80	27.84	66.44	33.54	22.15	16.45									

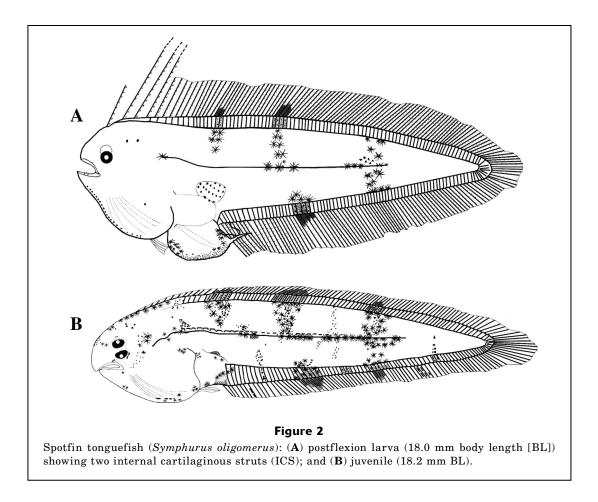
(Fig. 1B). Notochord flexion begins in larvae larger than 7 mm BL and ends near 15 mm BL (Table 3). In the only postflexion larva collected (18 mm BL), the right eye had begun to migrate to the left side of the head (Fig. 2A). In the juvenile stage (15.8–18.2 mm BL) the protruding gut is incorporated within the ventral body profile and migration of the right eye is complete. Most of the body of the juvenile has very small ctenoid scales; each scale has a single denticle; the swim bladder, pectoral fins, and the conical appendix are no longer visible; and head length is 25% of the BL.

Pigmentation Preflexion larvae (1.6–3.0 mm BL) typically have three equidistant blotches on the distal margin of the dorsal fin fold, located approximately between myomeres 6–9, 16–19, and 28–33, and an additional blotch located on the dorsal margin of the body between myomeres 28 and 33. There are two blotches present on the distal margin of the anal fin fold and two blotches on the ventral margin of the body located at myomeres 16–19 and at myomeres 27–36. Several small star-shaped melanophores form a line along the ventral

margin of the intestinal sac, nine similar melanophores are present on the left side of the gut, and three or four melanophores are present on the left side of the conical appendix (Fig. 1A).

Larvae 3.4-3.8 mm BL have a pigmentation pattern similar to that described above, but with slight changes in the numbers of myomeres forming the blotches (Fig. 1B); pigmentation is also more intense on the ventral area of the intestinal sac, where eight small star-shaped melanophores are located nearly at the distal margin of the left side of the anus. Small star-shaped melanophores are also present on the pectoral fins: three or more on the distal margin of the surrounding membrane of the pectoral fins, two or more on the distal region of the pectoral fin bud, and one on the pectoral fin base. Four similar melanophores are present on the swim bladder and several dot-like melanophores form a discontinuous line along the ventral margin of the axial musculature that does not reach the tip of the notochord (Fig. 1B).

Conspicuous at flexion stage are three vertical bands of star-shaped melanophores aligned perpendicular



to the notochord (Fig. 1C). These bands begin on the dorsal and ventral margins of the body and extend toward the body midline (Fig. 1C). The pigment pattern consists of two incomplete and one complete band on the left side of the body, located approximately equidistant from each other. The most anterior band overlies the bases of dorsal-fin pterygiophores 11-19 and extends to midway between the dorsal margin and the body midline; the second incomplete band overlies the bases of dorsal-fin pterygiophores 29-35 and extends to the body midline; the third band is complete and overlies the bases of dorsal-fin pterygiophores 53-63. Two or three star-shaped melanophores overlie the notochord below the second dorsal band and three or four other similar melanophores overlie the notochord below the third dorsal band. The first ventral band is located on the bases of the anal-fin pterygiophores 19–27 and the second ventral band is located on the bases of the analfin pterygiophores 39-48. Two discontinuous series of dashed pigments are located on the anal fin; one lies over the bases of pterygiophores 9-70; the second series occurs on the bases of the anal-fin rays 1 to 45 and covers almost two-thirds the length of the postabdominal region (Fig. 1C).

Head pigment is first present in flexion-stage larvae. Two to four star-shaped melanophores are located on the dorsal margin of the brain; all are equidistant from each other and located between the first and fourth dorsal-fin rays (Fig. 1C). A comparison of specimens preserved in formalin and ethyl alcohol revealed that the first and fourth melanophores fade in specimens in the formalin solution. Two internal melanophores are present in the posterior head region; one is located in the middle of the cleithrum near the base of the pectoral bud and the second is located on the base of the brain near the cleithrum. The left side of the head also has three series of small star-shaped melanophores. The first series (visible in specimens preserved with formalin and ethyl alcohol) extends along the ventral head margin from the lower jaw tip to the pelvic fin base. The second series (visible only in specimens preserved with ethyl alcohol) forms 'V' located along the ventroposterior margin of the jaw to the ventroposterior margin of the eye. The third series (visible only in specimens preserved with ethyl alcohol) begins at the bases of the first branchiostegal rays and extends posteriorly to the cleithrum. One prominent pigment blotch is present between the fourth and fifth branchiostegal rays. Both upper and lower jaws have four to five star-shaped melanophores at the posterior region.

Several small, star-shaped melanophores are present on the pectoral fins of flexion larvae: two or more occur on the base, three or more on the external margin of the surrounding membrane, and two or more in the

middle of the pectoral-fin bud. Most of these pigments are lost in specimens preserved in formalin. Nine or more similar melanophores are also present on the swim bladder.

The pigmentation of postflexion larvae (Fig. 2A) is similar to that of flexion-stage larvae (Fig. 1C). The major difference in pigmentation between flexion and postflexion larvae is the increase in the extent of the dorsal and ventral bands of star-shaped melanophores which extend towards the midline of the body, as well as to the dorsal- and anal-fin rays. One solid dark line extends down the midline of the body over the notochord from the first vertebra towards the end of the third dorsal band. One star-shaped melanophore appears above the first vertebra (Fig. 2A).

The pigmentation pattern of the juvenile specimens is similar to those of late postflexion specimens (Fig. 2, A and B). In the juvenile stage, formation of the three bands on the dorsal margin and two bands on the ventral margin of the body reach their greatest extension in length and width. These pigment bands extend over the dorsal and anal fins, covering half to two-thirds of the fin rays (Fig. 2B).

One discontinuous dashed line of melanophores is present on the body midline over the notochord extending from the posterior region of the brain to the posterior third of the postabdominal region. A second solid dark line is observed down the midline of the body over the notochord from the posterior of the brain towards the end of the third dorsal band (Fig. 2B).

Clusters of small star-shaped melanophores are present near the anteriormost section of this series and another group between the first and second dorsal bands. Additionally, small star-shaped melanophores form an inverse 'Y' between the second and third dorsal bands; this group of pigments extends from the base of dorsal-fin rays 46 and 47 toward the first ventral band, where it forks near the midline of the body but never reaches the base of the anal fin.

The pigmentation in the cephalic region increases dramatically during the transformation to the juvenile stage especially on the dorsal margin of the head, around the eyes, and ventrally in the branchial and pelvic region (Fig. 2B). On the stomach, four groups of star-shaped melanophores are present on the anterodorsal section, the posterodorsal section, the posteroventral section and the near pelvic-fin base (Fig. 2B).

Unpaired fin development In early preflexion larvae, the dorsal, anal, and caudal fin folds are wide and distinct. The dorsal fin fold begins behind the brain area (Fig. 1A). In larger, preflexion larvae, the first three dorsal fin rays are inserted at the level of the posterior margin of the brain (Fig. 1B). In flexion larvae, the second, third, and fourth dorsal fin rays are elongate and almost all specimens have all the rays in dorsal and anal fins formed. The caudal fin is incomplete, with only three or four rays (Fig. 1C). In postflexion larvae by 18 mm BL, all unpaired fins are completely formed (Fig. 2A).

Paired fin development From the preflexion to postflexion stages, the pectoral fins are fanlike, and have a massive fin lobe and surrounding membrane. During the flexion stage, the pelvic fins become apparent, but are not well developed and contain only the rudiments of four rays. In postflexion larvae, the pelvic fin rays are completely formed (Fig. 2A). During the juvenile stage, the pectoral fins are absorbed (Fig. 2B).

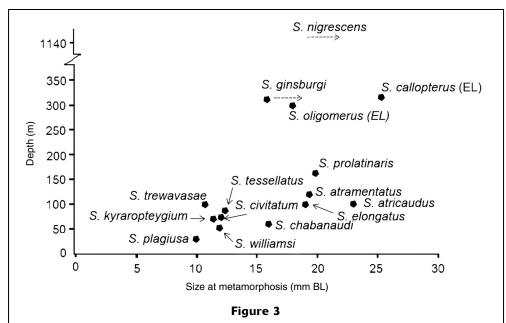
Discussion

Tonguefishes of the central-eastern Pacific are placed in a single genus (*Symphurus*) comprising 18 species. Previous studies have indicated the problems for identification of *Symphurus* species with overlapping meristic and morphometric characteristics and there have been few taxonomic studies of this genus. Insertion patterns of dorsal pterygiophores between dorsal neural spines (ID pattern) have proved to be useful in identifying members of this complex group if the ID pattern is combined with traditional meristic and morphometric characteristics (Munroe, 1992; Munroe et al., 1995).

The pigmentation pattern in early preflexion larvae of S. oligomerus is similar to that found in preflexion larvae (6.5 mm BL) of S. atricaudus (Charter and Moser, 1996) and S. williamsi (2.2 mm BL) by Aceves et al. (1999). However, S. atricaudus has up to four blotches on the dorsal and anal finfolds and S. williamsi has three melanophores along the dorsal margin of the body. two or three melanophores on the dorsal finfold, three melanophores along the ventral margin of the body, and one or two similar melanophores on the anal finfold. At this stage, it is not possible to distinguish the pigmentation patterns of early preflexion larvae of S. callopterus (Evseenko, 1990), S. elongatus (Charter and Moser, 1996), S. chabanaudi and S. prolatinaris (Evseenko and Shtaut, 2000), and S. atramentatus (Saldierna-Martínez et al., 2005) because the required diagnostic information is unavailable in the literature.

The pigmentation pattern in flexion larvae of *S. oligomerus* typically is composed of three oblique bands beginning in the dorsal margin of the body and running toward to the midline of the body. Only the third band reaches the mid line of the body. There is an oblique band on the ventral margin converging at the lateral midline with the third band of the dorsal margin and these two together have the appearance of a belt (Fig. 1C). This type of pigmentation is very similar to that described for flexion larvae of *S. callopterus* (7.5 mm SL), but *S. callopterus* has one more oblique band than *S. oligomerus*, which also has a larger abdominal projection (Evseenko, 1990).

All larvae Symphurus species from the eastern Pacific that have been described can be placed into three main groups based on pigmentation patterns (Saldierna-Martínez et al., 2005): 1) those with blotches on the dorsal and ventral margins of the body, such as S. elongatus (Charter and Moser, 1996), S. williamsi (Aceves et al., 1999), S. chabanaudi, and S. prolatinaris (Evseenko



Size at metamorphosis recorded for species of *Symphurus* plotted against maximum depth distribution for adults of the same species. Arrows indicate that metamorphosis should occur at larger size because data in the graphic for these two species correspond to the largest postflexion larva described (source: Kyle, 1913; Evseenko, 1990; Schneider, 1990; Kurtz and Matsuura, 1994; Munroe et al., 1995; Munroe, 1998; Aceves et al., 1999; Evseenko and Shtaut, 2000; Saldierna-Martínez et al., 2005; Farooqi et al., 2006; Fahay, 2007). EL=exterilium larvae.

and Shtaut, 2000); 2) those with a discontinuous series of dash-like melanophores on the dorsal and ventral margins of the body, such as *S. atricaudus* (Charter and Moser, 1996) and *S. atramentatus* (Saldierna-Martínez et al., 2005); and 3) those with heavily pigmented oblique bands extending from the dorsal to the ventral margins of the body, such as occurs in *S. callopterus* (Evseenko, 1990) and *S. oligomerus* (this study).

In addition to the three groups categorized by pigment patterns, Saldierna-Martínez et al. (2005) categorized Symphurus spp. larvae by the number of elongate dorsal-fin rays and the ID pattern as 1) those with 0-3 elongate dorsal-fin rays and the 1-5-3 ID pattern; 2) those with 5 elongate dorsal-fin rays and the 1-3-3 ID pattern; and 3) those with 7 elongate dorsal-fin rays and the 1-4-3 ID pattern. Saldierna-Martínez et al. (2005) suggested that the number of elongate dorsalfin rays is a derived character, as was also suggested by Hensley and Ahlstrom (1984). Our study showed that the three elongate dorsal-fin rays in S. oligomerus are associated with the 1-3-2 ID pattern, which does not correspond to previously established findings and indicates a high variability for this characteristic, thus reducing its value for phylogenetic interpretation among cynoglossids.

Larvae of *S. oligomerus* have a slightly compressed and ribbonlike body. The intestine, similar to that of *S. callopterus*, is an elongate and relatively slender sac with transparent walls that form a short and freely hanging abdominal projection ending in a short conical appendix. The length of the intestinal sac is almost one-quarter of the body length and is shorter than that in S. callopterus, which is almost one-half to two-thirds of the body length. In both species, the intestinal sac is supported by three cartilages. Larvae with this kind of intestine have been called exterilium larvae (Fraser and Smith, 1974; Moser, 1981); they are found in S. callopterus, at 7.5–21 mm SL, (Evseenko, 1990), and in some ophidiiform larvae (Gordon et al., 1984) that have a well-developed coracoid process (Fahay and Nielsen, 2003; Okiyama and Yamaguchi, 2004). The length of the loop intestine and the exterilium support of the intestinal tract in S. oligomerus and S. callopterus are useful features for differentiateing them from other central-eastern Pacific species of Symphurus.

An ontogenetic relationship within this genus is the apparent connection between size at metamorphosis and the depth range of adults. Saldierna-Martínez et al. (2005) found that species inhabiting deep waters usually are larger at metamorphosis than species inhabiting shallow waters. This relationship has been observed in several groups of fishes (Moser, 1981). It appears that species of *Symphurus* are not an exception (Fig. 3). At metamorphosis, *S. oligomerus* is 18 mm BL and adults inhabit waters down to 300 m (Mahadeva and Munroe, 1990; Munroe et al., 1995). In the Atlantic Ocean, *S. nigrescens* has been collected over an extensive vertical range (47–1140 m) on the

continental shelf and upper continental slope (Munroe, 1990) and the largest described larva of *S. lactea* (=*S. nigrescens*) is 8 mm NL (Kyle, 1913), indicating that size at metamorphosis should be bigger than 18 mm. In general, all species of *Symphurus* that inhabit depths below 300 m have the conical appendix at the end of the abdominal projection and at least two of them have exterilium larvae (Fig. 3). Descriptions by *S. ginsburgi* (Kurtz and Matsuura, 1994) and *S. nigrescens* do not mention whether they have exterilium larvae, but the shape of the intestine and the conical process would indicate so.

Exterilium larvae are found in several phylogenetically unrelated taxa (Ahlstrom et al., 1984). Species with exterilium larvae are hypothesized to benefit in several ways: 1) an increase in the length and surface area of the gut greatly enhances digestion in oligotrophic environments (Moser 1981); 2) the exterilium projection protects against predators because pigment patterns and the physical structure of this feature mimic siphonophores or poisonous coelenterates (Fraser and Smith, 1974; Moser, 1981; Gordon et al., 1984); and 3) the free intestinal loop acts as a specialized structure that prolongs pelagic life (Moser, 1981).

Acknowledgments

G.A.M. was supported by fellowships from Sistema Nacional de Investigadores and G.A.M. and R.S.M. by grants from Comisión de Operación y Fomento de Actividades Académicas and Estímulo al Desempeño de Investigación. The project was funded with grants from Centro Interdisciplinario de Ciencias Marinas-Instituto Politécnico Nacional, Secretaría de Investigación y Posgrado (SIP 20080918 and SIP 20090303), Consejo Nacional de Ciencia y Tecnología (FOSEMARNAT 2004-01-144 y SAGARPA 2007-117), y Comisión Nacional para el uso de la Biodiversidad (CONABIO-EC012). We thank Carlos Robinson and Instituto de Ciencias del Mar y Limnología at the Universidad Nacional Autónoma de México for their facilities to collect the zooplankton samples in the Gulf of California, as well as Thomas Munroe and all reviewers for their useful comments.

Literature cited

Aceves M. G., E. González, and R. J. Saldierna.

1999. Larval development of *Symphurus williamsi* (Cynoglossidae: Pleuronectiformes) from the Gulf of California. Fish. Bull. 97:738–745.

Ahlstrom, E. H.

1976. Maintenance of quality in fish eggs and larval collected during plankton hauls. *In* Zooplankton fixation and preservation (H. F. Steedman, ed.), p. 313–318. UNESCO Press, Paris.

Ahlstrom, E. H., K. Amaoka, D. A. Hensley, H. G. Moser, and B. Y. Sumida.

1984. Pleuronectiformes: Development. In Ontogeny and systematics of fishes (H. G. Moser, W. J. Richards, D. M.

Cohen, M. P. Fahay, A. W. Kendall, and S. L. Richardson, eds.), p. 640-670. Allen Press Inc., Lawrence, KS.

Charter, S. R., and H. G. Moser.

1996. Cynoglossidae: tonguefishes. *In* The early stages of fishes in the California Current region. CalCOFI Atlas 33 (H. G. Moser, ed.), p. 1408–1413. Allen Press, Inc., Lawrence, KS.

Evseenko, S. A.

1990. Unusual larvae of the marine tonguefish, Symphurus sp. (Cynoglossidae), from central waters of the eastern Pacific. J. Ichthyol. 30:148-154.

Evseenko, S. A., and M. I. Shtaut.

2000. Early stage of development of two species of tongue sole Symphurus chabanaudi and Symphurus prolatinaris (Cynoglossidae, Pleuronectiformes) from central eastern Pacific. J. Ichthyol. 40:751–761.

Fahay M. P.

2007. Early stage of fishes in the western North Atlantic Ocean (Davis Strait, Southern Greenland and Flemish Cap to Cape Hatteras). Vol. 2: Scorpaeniformes through Tetraodontiformes, p. 932–1696. Northwest Atl. Fish. Org., Nova Scotia.

Fahay, M. P., and J. G. Nielsen.

2003. Ontogenetic evidence supporting a relationship between *Brotulotaenia* and *Lamprogrammus* (Ophidiiformes: Ophidiidae) based on the morphology of exterilium and rubaniform larvae. Ichthyol Res. 50:209-220.

Farooqi T. W., R. F. Shaw, J. G. Ditty, and J. Lyczkowski-Shultz. 2006. Cynoglossidae: Tongue fishes, vol. II. In Early stages of Atlantic fishes: an identification guide for the western central North Atlantic (W. J. Richards, ed.), p. 2367–2379. CRC Press, Boca Raton, FL.

Fraser, T. H., and M. M. Smith.

1974. An exterilium larval fish from South Africa with comments on its classification. Copeia 1974:886-892.

Gordon, D. J., D. F. Markle, and J. E. Olney.

1984. Ophidiiformes: Development and relationships. *In* Ontogeny and systematics of fishes (H. G. Moser, W. J. Richards, D. M. Cohen, M. P., Fahay, A. W. Kendall Jr., and S. L. Richardson, eds.), p. 308–319. Allen Press, Inc., Lawrence, KS.

Hensley, D. A., and E. H. Ahlstrom.

1984. Pleuronectiformes: Relationships. *In* Ontogeny and systematics of fishes (H. G. Moser, W. J. Richards, D. M. Cohen, M. P., Fahay, A. W. Kendall Jr., and S. L. Richardson, eds.), p. 670-687. Allen Press, Inc., Lawrence. KS.

Kramer, D., M. J. Kalin, E. G. Stevens, J. R. Thrailkill, and J. R. Zweifel.

1972. Collecting and processing data from fish eggs and larvae in the California Current region. NOAA Tech. Rep. NMFS 370, 38 p.

Kurtz, F. W., and Y. Matsuura

1994. Early development of four tonguefishes of the genus *Symphurus* (Osteichthyes: Cynoglossidae) from the Southern Brazil. Japan. J. Ichthyol. 41(2):141–148.

Kyle, H. M.

1913. Flat-fish (Heterosomata). Rep. Dan. Oceanogr. Exped. Mediterr. 2(A):1-150.

Mahadeva N., and T. A. Munroe.

1990. Three new species of symphurine tonguefishes from tropical and warm temperate waters of the eastern Pacific (Sumphurus: Cynoglossidae: Pleuronectiformes). Proc. Biol. Soc. Wash. 103:931–954.

Moser, H. G.

1981. Morphological and functional aspects of marine fish larvae. *In* Marine fish larvae: morphology, ecology and relation to fisheries (R. Lasker, ed.), p. 89–131. Univ. Washington Press, Seattle.

1996. The early stages of fishes in the California Current region. CALCOFI Atlas 33, 1505 p. Allen Press, Inc., Lawrence, KS.

Munroe, T. A.

1990. Eastern Atlantic tonguefishes (*Symphurus*: Cynoglossidae, Pleuronectiformes), with descriptions of two new species. Bull. Mar. Sci. 47(2):464-515.

1992. Interdigitation pattern of dorsal-fin pterygiophores and neural spines, an important diagnostic character for symphurine tonguefishes (*Symphurus*: Cynoglossidae: Pleuronectiformes). Bull. Mar. Sci. 50:357–403.

1998. Systematics and ecology of tonguefishes of the genus *Symphurus* (Cynoglossidae: Pleuronectiformes) from the western Atlantic Ocean. Fish. Bull. 96:1–182.

Munroe, T. A., F. Krupp, and M. Schneider.

1995. Cynoglossidae. In Guia FAO para la identificación de especies para los fines de la pesca. Pacifico Centro-Oriental, vol. 2: Vertebrados-Parte 1 (W. Fischer, F. Krupp, W. Schneider, K. Carpenter, C. Summer, and V. Niem eds.), p. 1039-1059. FAO, Rome.

Munroe, T. A., and J. E. McCosker.

2001. Redescription of Symphurus diabolicus, a poorly-

known, deep-sea tonguefish (Pleuronectiformes: Cynoglossidae) from the Galápagos Archipelago. Rev. Biol. Trop. 49(suppl. 1):187–198.

Munroe, T. A., and D. R. Robertson.

2005. Symphurus ocellaris, a new shallow-water symphurine tonguefish collected off Pacific Panama (Pleuronectiformes: Cynoglossidae). Proc. Biol. Soc. Wash. 118(3):576–581.

Okiyama, M., and M. Yamaguchi.

2004. A new type of exterilium larva referable to Leptobrotula (Ophidiiformes: Ophidiidae: Neobythitinae) from tropical Indo-West Pacific. Ichthyol. Res. 51:77–80.

1984. Clearing and staining techniques. *In* Ontogeny and systematics of fishes (H. G. Moser, W. J. Richards, D. M. Cohen, M. P., Fahay, A. W. Kendall Jr., and S. L. Richardson, eds.), p. 35–37. Allen Press, Inc., Lawrence, KS.

Saldierna-Martínez, R. J., E. A. González-Navarro, and G. Aceves-Medina.

2005. Larval development of *Symphurus atramentatus* (Cynoglossidae: Pleuronectiformes) from the Gulf of California. Zootaxa 1016:1-14.

Schneider, W.

Potthoff, T.

1990. FAO species identification sheets for fishery purposes. Field guide to the commercial marine resources of the Gulf of Guinea. FAO, Rome.