

TWO UNUSUALLY LARGE PRE-TRANSITIONAL TONGUEFISH LARVAE (PLEURONECTIFORMES: CYNOGLOSSIDAE: *SYMPHURUS*) FROM OCEANIC WATERS NEAR THE GALÁPAGOS ISLANDS

Thomas A. Munroe and Trevor J. Krabbenhoft

ABSTRACT

Two, exceptionally large (51.0 and 36.6 mm SL), pre-transitional larval tonguefishes, collected in the water column and near surface waters overlying deep oceanic waters off the Galápagos Islands, are described and compared with larval stages and adults of eastern Pacific species of *Symphurus*. The larger specimen, *Symphurus varius* Garman, 1899, features a 1-3-3 pattern of interdigitation of proximal dorsal fin pterygiophores and neural spines (ID pattern), 12 caudal fin rays, 95 dorsal fin rays, 78 anal fin rays, 51 vertebrae, and 5 hypurals. This first known larval *S. varius* is also the largest known unmetamorphosed larva of the Cynoglossidae. The smaller larva is *Symphurus melanurus* Clark, 1936 based on its 1-5-3 ID pattern, meristic features, long protruding gut, and pigmentation. It represents the first known larva of *S. melanurus* and first occurrence of *S. melanurus* from the Galápagos Islands region. Whether large pre-transitional larvae are typical for *S. melanurus* and *S. varius*, or merely represent individuals having undergone delayed metamorphosis, will be confirmed when additional specimens become available. *Symphurus varius* is known only from the Galápagos Islands and other oceanic islands in the eastern tropical Pacific, thus capture of a larval *S. varius* near these offshore islands is not unexpected. Large size and oceanic occurrence of the pre-transitional stage *S. melanurus*, an inshore species, strongly suggest an expatriated individual from coastal seas having undergone delayed metamorphosis.

Larval tonguefishes (Cynoglossidae) are sometimes abundant in ichthyoplankton collections from tropical and warm-temperate seas off the Americas where they can constitute a significant proportion of the flatfish larvae (Ahlstrom, 1971; Farooqi et al., 2006). Relatively few ontogenetic series have been identified for members of this diverse family, which comprises well over 100 species (Munroe, 2005), and considerable work will be needed to accomplish this task. Of three genera currently recognized in the Cynoglossidae (Chapleau, 1988), only species of *Symphurus* occur in temperate and tropical seas of the Americas, where they are the most diverse genus of the Pleuronectiformes inhabiting these waters. Twenty-five species occur in the western Atlantic Ocean (Munroe, 1998; Saavedra-Díaz et al., 2003) and another 18 species inhabit marine and estuarine waters of the eastern Pacific Ocean (Munroe et al., 1995; Munroe and Robertson, 2005). The diversity of symphurine tonguefishes occurring sympatrically in tropical and warm-temperate regions of the New World, coupled with their large overlaps in morphometric and meristic characters, render identifications of these species problematic (Munroe, 1992, 1998), especially for larval stages (Kurtz and Matsuura, 1994; Farooqi et al., 2006). But, when combined with other features, the use of interdigitation patterns of proximal dorsal-fin pterygiophores with neural spines (ID pattern; Munroe, 1992) has facilitated identifications of symphurine tonguefish larvae (Yevseyenko, 1990; Aceves-Medina et al., 1999; Evseenko and Shtaut, 2000; Farooqi et al., 2006).

Only relatively recently has considerable progress been made in identifying and describing larval stages of eastern Pacific *Symphurus*. Since 1981, larvae and/or pre-settlement juveniles have been described or figured for nine of 18 eastern Pacific species of *Symphurus*, including those of *Symphurus atricaudus* (Moser, 1981; Ahlstrom et al., 1984; Matarese et al., 1989; Charter and Moser, 1996), *Symphurus callopterus* (as *Symphurus* sp.; Yevseyenko, 1990), *Symphurus elongatus* (Charter and Moser, 1996), *Symphurus williamsi* (Aceves-Medina et al., 1999), *Symphurus chabanaudi* (Beltrán-León and Rios-Herrera, 2000; Evseenko and Shtaut, 2000), *Symphurus gorgonae* and *Symphurus oligomerus* (Beltrán-León and Rios-Herrera, 2000), *Symphurus prolatinaris* (Evseenko and Shtaut, 2000), and *Symphurus atramentatus* (Saldierna et al., 2005).

Among earliest records of larval *Symphurus* from eastern Pacific waters is that of Kendall and Radcliffe (1912), who described and figured an unusually large larval tonguefish, USNM 65668 (37.9 mm SL; our measurement = 36.6 mm SL) collected in 1904 by the ALBATROSS “at the surface” overlying oceanic depths of 1000–1500 m off the Galápagos Islands. Kendall and Radcliffe (1912) tentatively identified this specimen as *S. atramentatus* based on counts for dorsal and anal fin rays (100 and 80, respectively) and its capture location, where only *S. atramentatus* was then known to occur. They further commented that their identification was “not at all certain.” This same illustration, again labeled as *S. atramentatus*, was reproduced in subsequent publications (Fraser and Smith, 1974; Grove and Lavenberg, 1997), without further comment. And, neither the specimen, the original illustration, nor subsequent references reproducing this illustration, were mentioned in a recent work describing a larval series of *S. atramentatus* from the Gulf of California (Saldierna et al., 2005).

We reexamined the USNM specimen (including radiographs) described by Kendall and Radcliffe (1912) and compared it both with the description of an ontogenetic series (Saldierna et al., 2005) and with larval specimens of *S. atramentatus*, and concluded that the USNM specimen is not *S. atramentatus*. Additionally, another extraordinarily large (51.0 mm SL), pre-transitional tonguefish larva, also captured in oceanic waters near the Galápagos Islands, was found in the fish collection of the Scripps Institution of Oceanography (SIO 55-265). This specimen did not match descriptions for any larvae of eastern Pacific *Symphurus* or the USNM specimen. Since many deepwater flatfishes have large larvae (Kyle, 1913; Bruun, 1937; Amaoka, 1971; Moser, 1981), sizes and capture locations (over deep oceanic waters) of these two large larvae initially suggested they might belong to some deepwater *Symphurus*, such as *Symphurus diabolicus* or *Symphurus microlepis* (300–757 m and 530 m, respectively), rarely-captured, eastern Pacific tonguefishes (Garman, 1899; Mahadeva and Munroe, 1990; Munroe and McCosker, 2001) whose larvae are unknown.

Although faint remnants of chromatophores are visible on both larvae, they lack conspicuous pigmentation usually evident and useful for identification in other larval *Symphurus*. Radiographs of both specimens, however, revealed that bony elements were sufficiently ossified to detect ID patterns and other meristic and osteological features that permitted identifications with a high degree of confidence as *Symphurus melanurus* (drab tonguefish) and *Symphurus varius* (mottled tonguefish). Osteological characters examined in these specimens also facilitated comparisons with descriptions of postflexion larvae of other eastern Pacific *Symphurus*, as well as comparisons with meristic features of all eastern Pacific *Symphurus* (Munroe, 1992; Munroe et al., 1995; Munroe and Robertson, 2005; T. Munroe, unpubl. data).

Herein, we describe morphological features of these specimens, provide supporting evidence for our identifications, compare these larvae to other species of eastern Pacific *Symphurus*, and provide comments regarding large-sized flatfish larvae.

MATERIALS AND METHODS

Methods for counts and measurements, as well as general terminology, follow those of Munroe (1998). Terminology for interdigitation patterns of proximal dorsal pterygiophores and interneural spines (ID pattern) follows that of Munroe (1992). ID pattern formulae reflect the numbers of proximal pterygiophores inserting into each respective interneural space beginning with the first (posterior to the first neural spine) and continuing posteriorly with each successive space to interneural space three. Thus, a 1-5-3 ID pattern would indicate one pterygiophore inserted into interneural space 1, 5 pterygiophores inserted into space 2, and 3 pterygiophores inserted into interneural space 3. A summary of meristic features for the two larvae and 18 species of eastern Pacific *Symphurus* appear in Table 1. Morphometrics, measured on the left side of each larva (except where noted), are presented in Table 2. Standard length (SL) was measured with digital calipers; all other measurements were taken to the nearest 0.1 mm using a microscope fitted with an ocular micrometer. Pectoral fin length was measured from the fin's anterior point of articulation with the body to its distalmost tip. Length of the protruding gut extended beyond the body's ventral profile (external gut of Fraser and Smith, 1974) was measured as the straight-line distance along the gut from the body margin at the ventro-posterior margin of the left opercle to the distalmost tip of the protruding gut. Body length (BL) refers to the measurement from the anterior end of the snout to end of the notochord in young larvae, or to the posterior margin of the hypural plate in more developed larvae (see Aceves-Medina et al., 1999). Conical appendix refers to a large cone-shaped protrusion on the abdominal appendage (see figs. in Kyle, 1913; Kurtz and Matsuura, 1994). Comparative materials of adults of species of eastern Pacific *Symphurus* were listed in Munroe (1992) and Munroe and Robertson (2005). Institutional codes for collections containing specimens follow those listed in Leviton et al. (1985). Taxonomic authorities for species names appearing in text and tables are listed in Appendix 1. Nomenclatural information for authors and dates of publication follows that contained in the online version of *The Catalog of Fishes* (Eschmeyer and Fricke, 2009).

Description of Pre-Transitional Larva of *Symphurus melanurus* (Figs. 1A–D; Tables 1, 2)

Material Examined.—USNM 65668, 36.6 mm SL, ALBATROSS Station 4640, 0°39.4' N, 88°11' W (near Galápagos Islands), taken with ichthyoplankton net at surface over 1000–1500 m, 6 November 1904.

Description.—ID pattern 1-5-3 (Fig. 1D). Caudal fin rays 12. Dorsal fin rays 102. Anal fin rays 83. Pelvic fin rays 4. Total vertebrae 54 (Fig. 1C); abdominal vertebrae 9 (3+6). Hypurals 4. Small ctenoid scales on posterior head and body; many missing precluding accurate count in longitudinal series. No scales evident on dorsal and anal fin rays. Morphometric information appears in Table 2.

A large (36.6 mm SL) pre-transitional larva (Figs. 1A–B). Body elongate and laterally compressed (Fig. 1A; Table 2); greatest depth (about 25% SL) in anterior one-fourth to about body midpoint, with gradual posterior taper. Head short (about 22% SL), wider than long (HW/HL = 1.2). Snout short, blunt, squarish, 2.4 times larger than eye diameter. Dermal papillae absent. Left side anterior nostril a short tube

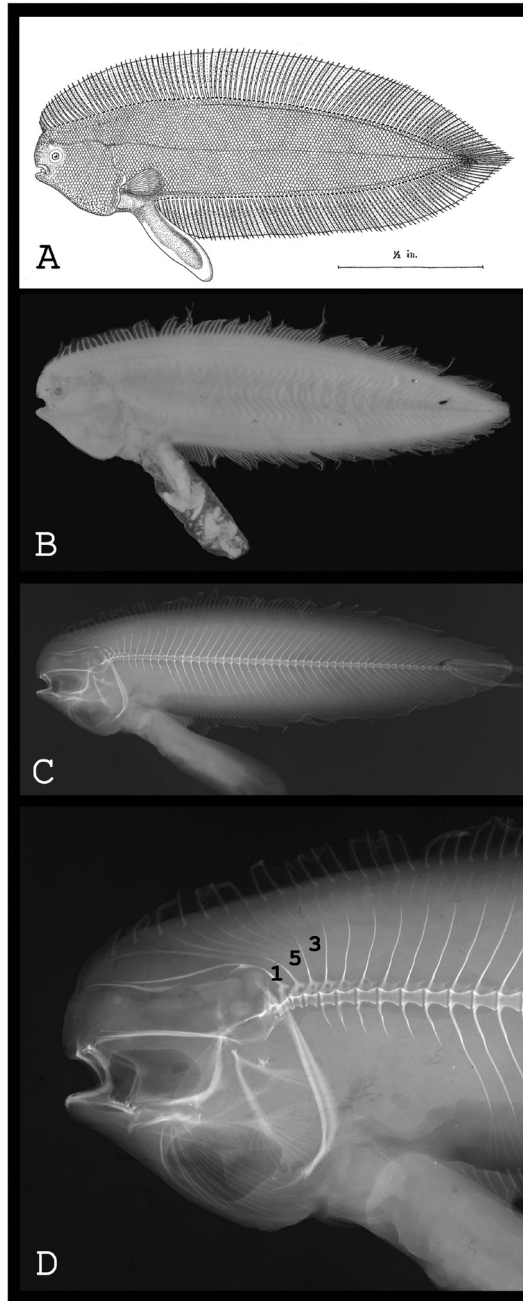


Figure 1. Illustration, photograph and radiographs of a pre-transitional larva of *Symphurus melanurus* (USNM 65668) collected in oceanic waters near the Galápagos Islands. (A) Original illustration from Kendall and Radcliffe (1912) of larval flatfish tentatively identified as *Symphurus atramentatus* (re-identified in present work as *Symphurus melanurus*). (B) Photograph of left side of same specimen. (Note blunt profile of anterior head, small eye and protruding gut.) (C) Radiograph of same specimen. (D) Radiograph illustrating 1-5-3 pattern of interdigitation of anterior proximal dorsal-fin pterygiophores and neural spines.

Table 1. Meristic data for 18 species of eastern Pacific *Symphurus* and pre-transitional larvae of *Symphurus melanurus* (USNM 65668) and *Symphurus varius* (SIO 55-265) (bold typeface). Comparison data modified from Munroe (1992) and Munroe and Robertson (2005).

Species	ID pattern	Caudal fin rays	Dorsal fin rays	Anal fin rays	Vertebrae	Hypurals
<i>S. gorgonae</i>	1-3-2	12	80–89	63–74	46–49	4
<i>S. oligomerus</i>	1-3-2	12	87–97	72–83	48–52	5
<i>S. microlepis</i>	1-3-2	12	106	92	57	5
<i>S. diabolicus</i>	1-3-2	12	109	94	58	5
<i>S. atramentatus</i>	1-3-3	12	89–98	75–82	49–53	4
<i>S. varius</i>	1-3-3	12	90–97	77–81	50–52	5
<i>S. varius</i> (larva)	1-3-3	12	95	78	51	5
<i>S. ocellaris</i>	1-3-4	12	96–97	80–81	51	4
<i>S. callopterus</i>	1-3-4	12	105–114	91–98	57–61	4
<i>S. fasciolaris</i>	1-4-3	10	90–97	75–80	48–52	4
<i>S. leei</i>	1-4-3	12	93–104	78–88	51–56	4
<i>S. melasmatotheca</i>	1-5-3	11	90–98	74–80	49–52	4
<i>S. undecimplerus</i>	1-5-3	11	97–105	80–87	52–56	4
<i>S. williamsi</i>	1-5-3	12	89–95	73–79	47–51	4
<i>S. atricaudus</i>	1-5-3	12	94–102	77–83	50–53	4
<i>S. melanurus</i>	1-5-3	12	96–104	79–87	50–54	4
<i>S. melanurus</i> (larva)	1-5-3	12	102	83	54	4
<i>S. chabanaudi</i>	1-5-3	12	98–109	82–92	52–57	4
<i>S. elongatus</i>	1-5-3	12	99–107	83–90	53–56	4
<i>S. prolatinaris</i>	1-5-3	12	103–110	86–93	54–58	4

dorsal to midpoint of upper jaw. Posterior nostril a small, scarcely noticeable, slit on snout anterior to eye. Upper jaw slightly longer than snout. Posterior margin of jaw about at vertical through anterior margin of pupil of left eye. Eyes noticeably small, round; asymmetrical. Left eye located dorsal to lower jaw, with most of its diameter posterior to vertical through posterior margin of jaw; obvious depression on snout dorsal and posterior to left eye (channel to accommodate migrating right eye?). Right eye superior in position to that of left eye, located closer to dorsal fin base than to upper jaw. Migration of right eye initiated as evidenced by its embedded position below lateral surface of head and dorso-medial orientation relative to lateral surface of head. Pupillary operculum absent. Postorbital length about 73% HL; slightly greater than width of upper head lobe. Upper head lobe width slightly larger than lower head lobe width (UHL/LHL = 1.1). Posterior margin of opercle with obvious medial notch; lower opercular lobe larger than upper opercular lobe. Dorsal, anal, caudal, pectoral and left pelvic fins completely developed. Predorsal length short, about 18% HL. Dorsal fin origin at vertical through anterior pupil of left eye; second dorsal fin ray about at vertical through middle of left eye. Anteriormost dorsal fin ray broken at mid point, slightly longer than succeeding fin rays, but not elongate. Successive dorsal fin rays approximately equal in length. Pectoral fins large, paddle-shaped, slightly subequal in size (left 13% SL, right about 9% SL), without fin rays, but with filamentous projections (up to 9 on right pectoral fin) along distal margins. Pelvic fin on ventral midline. Caudal fin rays developed, but broken at their mid-lengths.

Large, conspicuous, protruding gut extended beyond ventral margin of body cavity by about 21.4 mm (about 58% SL) and trailing posteriad from ventral margin of body (Figs. 1A–C). Intestine forming loop within, and extended to about 81% of length

of, protruding gut mass. Conical appendix absent. Anus just off body midline near ventral margin on right side of body.

Body yellowish-white (pigment mostly faded), with remnants of faint, irregular chromatophores overlying pterygiophores of dorsal and anal fin rays and along anterior and medial regions of horizontal septum on left side of body. Pigment asymmetrically developed; left side anterior snout with four, faded, stellate melanophores anterior to anterior nostril; several smaller melanophores dorsal to depression formed by channel for migration of right eye; left lower jaw and chin region with three rows of small, but conspicuous, faded (orange-brown) melanophores along ventral margin from tip of jaw to region about at vertical through posterior margin of left eye, and with single row of melanophores along ventral margin of head nearly to opercular opening; right side chin without melanophores. Cluster of eight melanophores anterior to base of first dorsal fin ray on left side and four melanophores anterior to base of first dorsal fin ray on right side. Left sides of dorsal and anal fins, especially anteriorly, with series of larger, irregular, faded (orange-brown) melanophores in dermis in spaces between fin ray bases; these melanophores located throughout entire lengths of dorsal fin and on anal fin from about anal fin ray 8 to posteriormost ray. Left sides of dorsal, anal, pelvic, and caudal fin rays also with series of smaller, faded (orange) melanophores on middle two-thirds of fin rays. Left side of caudal fin also with row of six, small, round melanophores across base of fin. Right sides of dorsal and anal fin rays with irregular series of small melanophores on fin membranes in distal half of fins; right sides of caudal fin rays with small number of faded (reddish-orange) melanophores scattered on basal two-thirds of fin. Pelvic fin rays with several, faded (reddish-orange) melanophores scattered throughout their lengths. Proximal one-third of anterior margin of protruding gut with a series of small, faded melanophores.

Remarks.—Kendall and Radcliffe (1912) briefly described and provided a figure (reproduced here as Fig. 1A) of a large (37.9 mm SL; their measurement) larval tonguefish collected by the ALBATROSS in the near-surface waters located over 1000–1500 m depth off the Galápagos Islands. They tentatively identified their specimen as *S. atramentatus*, and commented that this specimen was without color markings, the eye was just beginning to migrate from right to left side of the head, and this larva had a large protruding gut (incorrectly referred to as unabsorbed yolk-sac). Furthermore, they observed that such a large larval form must be abnormal. The figure of this larva was later reproduced in Fraser and Smith (1974) and Grove and Lavenberg (1997) and labeled as *S. atramentatus*, without further elaboration. In their recent description of a larval series of *S. atramentatus*, Saldierna et al. (2005) did not mention this larva, nor the figure appearing in Kendall and Radcliffe (1912) or other subsequent citations of this figure.

Our examination (including radiographs, see Figs. 1C–D) and comparisons of the ALBATROSS specimen with an ontogenetic series of *S. atramentatus* described by Saldierna et al. (2005) indicate it is not *S. atramentatus*. The primary difference between the ALBATROSS specimen and *S. atramentatus* is that the ALBATROSS specimen has a 1-5-3 ID pattern (Fig. 1D), whereas *S. atramentatus* has a predominant 1-3-3 ID pattern. None of 151 specimens of *S. atramentatus* examined by Munroe (1992) have a 1-5-3 ID pattern, nor do any of 14 specimens examined by Saldierna et al. (2005). In fact, among four species of *Symphurus* characterized by a predominant 1-3-3 ID pattern (Munroe, 1992), none of 293 specimens examined possess a 1-5-3 ID pattern. Thus, it appears unlikely that the USNM specimen is an *S. atramentatus*.

with an anomalous ID pattern. Furthermore, our counts (from radiographs) of dorsal and anal fin rays for this larva are also higher (102 and 83 vs 100 and 80, respectively) than those reported by Kendall and Radcliffe, and are just beyond ranges reported for *S. atramentatus* (Table 1). Additionally, this larva has 54 total vertebrae, whereas *S. atramentatus* typically features 49–53 total vertebrae ($n = 151$).

Eight species of *Symphurus*, all from the eastern Pacific Ocean, are characterized by the 1-5-3 ID pattern (Munroe, 1992). Except for *S. undecimplerus* and *S. melasmatotheca*, which have 11 caudal fin rays (see Table 1 and comparisons below), the other species (*S. williamsi*, *S. atricaudus*, *S. melanurus*, *S. chabanaudi*, *S. elongatus*, and *S. prolatinaris*) have the same number (12) of caudal fin rays as does the ALBATROSS specimen, and with exception of *S. williamsi* and *S. prolatinaris*, all have at least partially overlapping meristic features. Counts of dorsal and anal fin rays for the ALBATROSS specimen are well within ranges reported for *S. melanurus*, *S. chabanaudi* and *S. elongatus* (Table 1). Like *S. melanurus*, *S. chabanaudi* and *S. elongatus* are shallow-water tonguefishes with sympatric distributions from the Gulf of California to northern Peru (Munroe et al., 1995). None is reported from the Galápagos Islands or surrounding waters (Munroe et al., 1995; Grove and Lavenberg, 1997).

With nearly complete overlap in meristic features among *S. melanurus*, *S. chabanaudi*, and *S. elongatus* (Table 1), other characters are needed to distinguish the larval *S. melanurus* from these species. The ALBATROSS specimen clearly differs from the description and illustration of a pre-transitional larval (15.3 mm) *S. chabanaudi* (Evsenko and Shtaut, 2000; their fig. 2C) in lacking elongate dorsal-fin rays (vs two in *S. chabanaudi*). The ALBATROSS specimen also differs from the larval *S. chabanaudi* in its pigmentation, which consists of some irregular pigmentation along its right-side horizontal myoseptum (pigment present in larvae of several other species of *Symphurus*) but without any trace of the large, well-defined black smudge on the middle body featured in the 15-mm larval *S. chabanaudi*. The ALBATROSS specimen also has obvious melanophores in the integument between bases of the dorsal and anal fin rays that are apparently absent in the pre-transitional larval *S. chabanaudi*. And, the ALBATROSS specimen does not have the longitudinal series of about four clusters of melanophores along its dorso-lateral body evident in the larval *S. chabanaudi*. The larval *S. melanurus* also differs in its extremely long ($> 50\%$ SL) and slender, ventro-posteriorly oriented protruding gut (Fig. 1B) compared with the shorter (about 25% SL) and more ventrally oriented protruding gut in *S. chabanaudi*. It may also have a smaller pectoral fin than that of *S. chabanaudi*, but more observations on both species are needed.

The ALBATROSS specimen has a body and head shape and similar-sized pectoral fins that are nearly identical to those illustrated for a smaller (18.9 mm), pre-transitional larval *S. elongatus* (Charter and Moser, 1996; their fig. 2), and the pre-transitional larvae of both species lack elongate dorsal fin rays. But, the ALBATROSS larva also has a much longer protruding gut ($> 50\%$ SL) than that of *S. elongatus* (about 25% SL), has filamentous projections on distal margins of its pectoral fins (not described for larval *S. elongatus*), and has small melanophores in the dermis between bases of its dorsal fin rays (not described for larval *S. elongatus*).

Based on ID pattern, meristic features, head shape, pigmentation features, and relative size of the protruding gut, we identify the ALBATROSS specimen as a pre-transitional larva of *S. melanurus*, a common, wide-ranging and shallow-water (4–31 m) species occurring on the inner continental shelf from the Gulf of California to

northern Peru (Munroe et al., 1995). This specimen represents the first confirmed larval stage for *S. melanurus*, and it also records the first occurrence of *S. melanurus* from the Galápagos Islands region. Heretofore, this species has not been reported from the Galápagos Islands or other eastern Pacific oceanic islands. Thus, capture of this large larval *S. melanurus* over deep oceanic waters offshore of the Galápagos Islands is unusual and strongly suggests the possibility that it had been transported offshore and expatriated from populations residing in coastal waters along the continent.

Beltrán-León and Rios-Herrera (2000) described transformed specimens of *S. melanurus*, and our examination of juveniles reveals several similarities between larval and juvenile life stages. First, the larval *S. melanurus* has a blunt head (Fig. 1A) similar to that of juvenile *S. melanurus*. Secondly, despite Kendall and Radcliffe's assertion that the ALBATROSS specimen was "without color-markings," we observed faint pigment in the dermis between bases of dorsal and anal fin rays. These melanophores, though faded, were especially apparent in the anteriormost dorsal fin. This pigmentation feature mirrors the condition in juvenile *S. melanurus*, and distinguishes this larva from those of both *S. chabanaudi* and *S. elongatus*, which apparently lack these spots.

Comparisons.—Among other species with the 1-5-3 ID pattern, the larval *S. melanurus* differs from *S. undecimplerus* and *S. melasmatotheca* in having 12 (vs 11) caudal fin rays. Meristic features of this larva are also much higher than those of *S. melasmatotheca* (Table 1).

The larval *S. melanurus* differs most obviously from larval *S. williamsi* (Aceves-Medina et al., 1999) in lacking elongate dorsal fin rays (vs three in *S. williamsi*), in having a blunt, squarish anterior head profile (vs head much more rounded in *S. williamsi*) and a longer (vs shorter) protruding gut. The larval *S. melanurus* also has distinctly higher meristic features than those of *S. williamsi* (102 vs 89–95 dorsal fin rays; 83 vs 73–79 anal fin rays; and 54 vs 47–51 vertebrae in *S. williamsi*).

The larval *S. melanurus* is easily distinguished from *S. prolatinaris* by its lower, and non-overlapping, dorsal and anal fin ray counts (Table 1). Additionally, it differs from a pre-transitional larva of *S. prolatinaris* (Evseenko and Shtaut, 2000) in lacking elongate dorsal fin rays (vs 2 elongate dorsal fin rays in *S. prolatinaris*) and it also has a much longer protruding gut (58% vs < 25% of SL).

The larval *S. melanurus* has some similarities to those of larval *S. atricaudus* (Matarese et al., 1989; Charter and Moser, 1996) in that both feature a long protruding gut trailing ventroposteriorly from the abdomen. The larval *S. melanurus* differs from postflexion *S. atricaudus* in having a blunt, squarish anterior head profile (vs head more rounded in *S. atricaudus*), a smaller eye (about 8% HL vs 13%–15% HL in *S. atricaudus*), and 54 total vertebrae (vs 50–53 in *S. atricaudus*). The larval *S. melanurus* also lacks the distinctive series of pigmented blotches along dorsal and ventral margins of the body, and lacks the dark pigment on the trailing gut, both of which are evident in larval *S. atricaudus* (Matarese et al., 1989). The larval *S. melanurus* has small pigmented spots scattered over middle surfaces of the left sides of its dorsal and anal fins; in contrast, postflexion larval *S. atricaudus* have pigmented speckles clustered near distal margins of the dorsal and anal fins.

All other eastern Pacific species have ID patterns and/or numbers of fin rays and total vertebrae different from those of the larval *S. melanurus* (Table 1).

Description of Pre-Transitional Larva of *Symphurus varius*
(Figs. 2A–D; Tables 1, 2)

Material Examined.—SIO 55-265 (51.0 mm SL): 0°02'S, 100°23'W, HORIZON, 6 December 1955; collected in ichthyoplankton net towed obliquely between 730 fathoms and the surface (1344–0 m).

Description.—ID pattern 1-3-3 (Fig. 2C). Caudal fin rays 12. Dorsal fin rays 95. Anal fin rays 78. Pelvic fin rays 4. Total vertebrae 51; abdominal vertebrae 9(3+6). Hypurals 5 (Fig. 2D). Body and head covered with very small, ctenoid scales. No scales evident on dorsal and anal fin rays. Accurate scale counts not available, but specimen with 100+ scales in longitudinal series. Morphometric information appears in Table 2.

A large (51.0 mm SL), pre-transitional larva (Figs. 2A–B). Body elongate and laterally compressed; greatest depth (about 28% SL; Table 2) in anterior one-fourth to about body midpoint, with body depth tapering gradually posteriorly. Head short (19% SL), wider than long (HW/HL = 1.2). Snout short, round; snout length longer than eye diameter (SNL/ED = 1.8). Dermal papillae absent. Left side anterior nostril a short tube dorsal to midpoint of upper jaw. Posterior nostril a small slit, scarcely noticeable, on snout anterior to eye. Upper jaw slightly longer than snout. Posterior margin of lower jaw about at vertical through anterior margin of pupil. Eyes small, round; asymmetrical; without pupillary operculum. Left eye dorsal to, and mostly posterior to, posterior margin of lower jaw. Right eye superior in position compared with that of counterpart; located just slightly dorsal to mid-distance between dorsal fin base and lower jaw, in advance of vertical through anterior base of first dorsal fin ray. Right eye visible just above left eye when viewed through semi-transparent area of skin on left side of head. Migration of right eye initiated as evidenced by its embedded position below lateral surface of head (vs non-migrated eye with lateral surface extending beyond lateral surface of integument) and dorso-medial orientation relative to lateral surface of head. Postorbital length about 76% HL; nearly equal to width of upper head lobe. Upper head lobe much larger than lower head lobe (UHL/LHL = 1.6). Posterior margin of opercle deeply notched at about its midpoint; lower and upper opercular lobes equal in size. Dorsal, anal, caudal, pectoral, and pelvic fins completely formed. Predorsal length about 20% HL. Anteriormost dorsal-fin rays not elongate; their bases with greater diameter and spaced farther apart than those of more posterior rays. Origin of first dorsal fin ray posterior to vertical through posterior margin of left eye; first dorsal fin ray about 1/6 length of second dorsal fin ray. Third and fourth dorsal fin rays only slightly longer than more posterior rays. Both pectoral fins well developed, paddle-shaped, without fin rays; approximately equal in size (about 4% SL). Pelvic fin on ventral midline. Caudal fin rays developed.

Large, conspicuous protruding gut extended beyond ventral margin of body cavity and trailing posteriorly along body (Fig. 2A); length of protruding gut approximately 6.4 mm (about 13% SL). Intestine forming loop within, and extending most of way (about 86% of length) into, protruding gut mass. Conical appendix absent, but distal-most tip of protruding gut with small rounded process (remnant of conical appendix?). Anus just off body midline near ventral margin on right side of body.

Body uniformly yellowish-tan (pigmentation nearly completely faded?), with a small number of faint (reddish-orange) melanophores scattered on several dorsal and anal fin rays in anterior and middle regions of these fins.

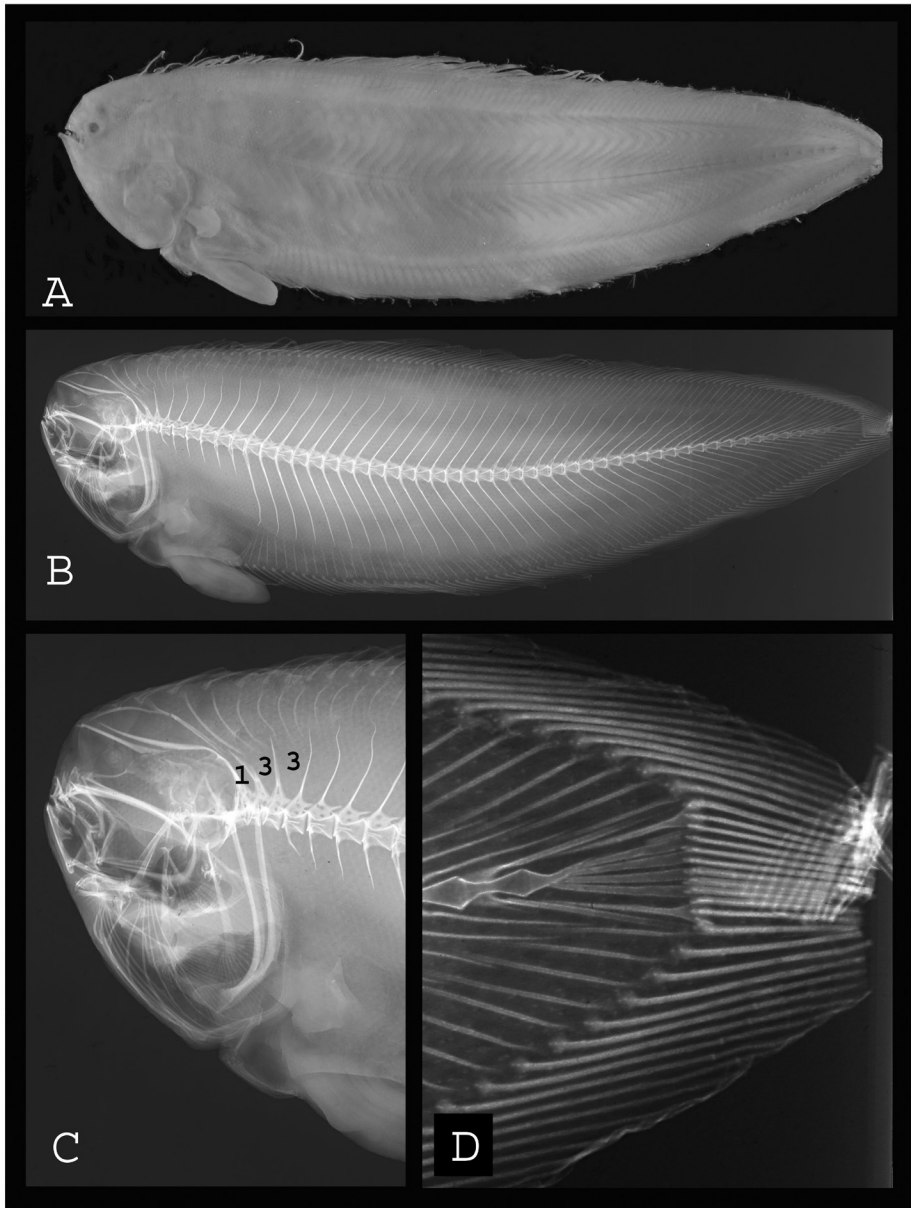


Figure 2. Photograph and radiographs of a pre-transitional larva of *Symphurus varius* (SIO 55-265, 51.0 mm SL) collected in oceanic waters near the Galápagos Islands. (A) Photograph of left side of specimen. (B) Radiograph of same specimen. (C) Radiograph depicting 1-3-3 pattern of interdigitation of anterior proximal dorsal-fin pterygiophores with neural spines. (D) Radiograph of same specimen depicting caudal skeleton with five hypurals (four ventralmost of nearly uniform size and dorsalmost hypural shorter than others).

Table 2. Morphometric features for single specimens of large-sized, pre-transitional larvae of *Symphurus melanurus* (USNM 65668) and *Symphurus varius* (SIO 55-265) collected in oceanic waters near the Galápagos Islands.

Character	<i>Symphurus melanurus</i>			<i>Symphurus varius</i>		
	Measurement (mm)	%SL	%HL	Measurement	%SL	%HL
Standard length	36.6			51.0		
Body depth	9.3	25.4	--	13.6	26.7	--
Preanal length	7.7	21.0	--	13.1	25.7	--
Protruding gut length	21.4	58.5	--	6.4	12.5	--
Intestine within gut	17.4	47.5	--	5.1	10.0	--
Predorsal length	1.5	4.0	18.3	1.9	3.7	19.6
Pelvic-fin length	4.9	13.4	59.8	2.9	5.7	29.9
Caudal-fin length	--	--	--	--	--	--
Left pectoral fin	4.6	12.6	56.0	2.3	4.5	23.7
Right pectoral fin	3.1	8.5	37.9	2.3	4.5	23.7
Head length	8.2	22.4	--	9.7	19.0	--
Head width	10.2	27.9	--	11.4	22.4	--
Postorbital length	6.9	16.4	73.2	7.4	14.5	76.3
Upper head lobe	5.2	14.2	63.4	7.6	14.9	78.4
Lower head lobe	4.9	13.4	59.8	4.9	9.6	50.5
Snout length	1.7	4.6	20.7	1.4	2.7	14.4
Upper jaw length	1.8	4.9	22.0	1.7	3.3	17.5
Eye diameter	0.7	1.9	8.5	0.8	1.6	8.2
Chin depth	0.7	1.9	8.5	1.6	3.1	16.5
Upper opercular lobe	1.9	5.2	23.2	2.4	4.7	24.7
Lower opercular lobe	3.1	8.5	37.8	2.4	4.7	24.7

Remarks.—The general absence of pigmentation in the SIO larva and its large size limit comparisons with larvae of other eastern Pacific tonguefishes. But, ID pattern and other meristic features are well developed in this larva, and these proved critical for identifying and diagnosing it. Among eastern Pacific *Symphurus*, meristic features of the SIO larva are most similar to those of *S. atramentatus*, the only other species with a 1-3-3 ID pattern, and *Symphurus ocellaris*, which has a 1-3-4 ID pattern (Table 1). The SIO larva differs from both species in having five hypurals (vs 4 in *S. atramentatus* and *S. ocellaris*), a highly conserved feature in species of *Symphurus*. Larvae of *S. ocellaris* are unknown, but those for *S. atramentatus* were described recently (Saldierna et al., 2005) based on specimens collected in the Gulf of California. The SIO larva differs further from larval *S. atramentatus* in lacking elongate dorsal fin rays (postflexion larvae of *S. atramentatus* with five elongate dorsal fin rays). The length of the intestine in the protruding gut is more than twice the head length in the SIO larva (vs intestine size nearly equal to cephalic length in *S. atramentatus*), and at a BL of 20.2 mm, the gut has retracted into the ventral body profile in larval *S. atramentatus*, while the SIO larva still features a conspicuous protruding gut.

Based on its 1-3-3 ID pattern, 5 hypurals, other meristic characters, and its long protruding gut, we identify this larva as *S. varius*, a tonguefish inhabiting moderately deep waters (78–278 m) around eastern Pacific oceanic islands including those of the Galápagos Archipelago (Munroe et al., 1995; Grove and Lavenberg, 1997; Munroe and McCosker, 2001), and at Cocos and Malpelo islands (Garman, 1899; Munroe et al., 1995). This first known larval stage of *S. varius* is the largest unmetamorphosed

larva of the Cynoglossidae, and far exceeds sizes we observed while examining several hundred larval cynoglossids or those reported in the literature. Large size, ocular asymmetry (dorsal placement, slight embedding and dorsal orientation of right eye), and absence of elongate anterior dorsal fin rays indicate metamorphosis had already initiated in this specimen at time of its capture. Since no other larval *S. varius* are known, it is difficult to determine whether large pre-transitional larvae are typical of this species. Of interest though, is the size of this larva relative to lengths of both juvenile *S. varius* captured in benthic collecting gear and especially sizes of some of the smaller mature females (T. Munroe, unpubl. data). This pre-transitional larva exceeds sizes of 7/9 juveniles (41.3–59.5 mm SL) taken in benthic gear. Additionally, its length is nearly 85% of that of the smallest female (59.5 mm SL) just beginning to mature (ovaries starting posterior elongation), and measures about 80%–82% of the lengths (59.2–63.6 mm SL) of three other females either fully mature (ovaries elongate with many obvious ova) or approaching full maturity (elongate ovaries with some ova evident).

Juvenile and adult *S. varius* occur in relatively deep waters (78–278 m) around several eastern Pacific oceanic islands including the Galápagos Archipelago (Munroe et al., 1995; Grove and Lavenberg, 1997; Munroe and McCosker, 2001), and Cocos and Malpelo islands (Garman, 1899; Munroe et al., 1995). Since adults of this species have been reported previously from the Galápagos Islands, capture of a larval *S. varius* offshore of these islands would not be unexpected.

Larvae of some species of *Symphurus* have an obvious conical appendix protruding from the distal tip of their abdomens. Kyle (1913) first described the conical appendix in larval *Symphurus lacteus* (= *Symphurus nigrescens* Rafinesque, 1810), although earlier illustrations of larval *Symphurus* (e.g., Emery, 1879) also clearly depicted this character. Though its function is unknown, presence or absence of the conical appendix has value in identifying larvae of some *Symphurus* (Kyle, 1913; Kurtz and Matsuura, 1994). For example, of nine eastern Pacific species for which larvae have been described, only larval *S. callopterus* (Yevseyenko, 1990) have a conical appendix. The larval *S. varius* lacks an obvious conical appendix, but has a small rounded process present at the distalmost tip of its protruding gut that could represent remnants of a nearly resorbed conical appendix, although available data indicate the conical appendix is not resorbed until the protruding gut retracts into the body cavity, which occurs around time of settlement. In a relatively complete ontogenetic series of larvae of the western South Atlantic *Symphurus ginsburgi*, larvae of all stages clearly possessed this character (Kurtz and Matsuura, 1994), as do all larval stages of the eastern Atlantic *S. nigrescens* (Kyle, 1913). From these two examples, it seems unlikely that the process in *S. varius* represents the remnants of a conical appendix, however, given the possibility that this extremely large pre-transitional larva may have undergone delayed metamorphosis, more specimens must be examined before it can be ascertained that larval *S. varius* lack a conical appendix.

Comparisons.—Of the remaining 12 species of eastern Pacific *Symphurus* with 12 caudal fin rays, only five (*S. oligomerus*, *S. leei*, *S. williamsi*, *S. atricaudus*, and *S. melanurus*) have counts for dorsal and anal fin rays, or vertebral counts, that are similar to those observed in the larval *S. varius* (Table 1). With its 1-3-3 ID pattern and five hypurals, the larval *S. varius* is easily distinguished from *S. williamsi*, *S. atricaudus*, and *S. melanurus*, all featuring the 1-5-3 ID pattern and 4 hypurals. Individuals (n = 821) belonging to species of *Symphurus* with the predominant 1-5-3

ID pattern do not have a 1-3-3 ID pattern or five hypurals (Munroe, 1992). Thus, it appears highly unlikely that this is a larval *S. williamsi*, *S. atricaudus*, or *S. melanurus* with an anomalous ID pattern. *Symphurus oligomerus* and *S. leei* also feature ID patterns different than that of the larval *S. varius* (1-3-2 in *S. oligomerus* and 1-4-3 in *S. leei*), and *S. leei* has only 4 (vs 5) hypurals.

DISCUSSION

At 51.0 and 36.6 mm SL, these pre-transitional larvae are among, if not the, largest cynoglossid larvae reported to date, and are considerably larger than transitional specimens (7–29 mm) described for other species of *Symphurus* (Kyle, 1913; Bini, 1968; Olney and Grant, 1976; Kramer, 1991; Kurtz and Matsuura, 1994; Charter and Moser, 1996; Farooqi et al., 2006). Prior to this study, the largest known larval *Symphurus* was a 25.4 mm SL pre-transitional specimen of *S. callopterus* (Yevseyenko, 1990). Moser (1981, 1996) noted that the greatest size range of teleost larvae (including some of the largest larvae) is found in flatfishes. Large larvae are known in a variety of flatfish taxa including *Bothus lunatus* (to 35 mm SL; Evseenko, 2008) and *Bothus ocellatus* (to 42 mm TL; Colton, 1961), *Poecilopsetta beanii* (to about 36 mm; Lyczkowski-Shultz, 2006), *Glyptocephalus zachirus* (49–59 mm SL based on Matarese et al., 1989; to 72 mm SL, Ahlstrom et al., 1984; to 89 mm SL, Pearcy et al., 1977), *Laeops nigromaculatus* (to 63 mm SL; Kaga and Amaoka, 2003), *Microstomus pacificus* (up to 75 mm SL; Markle et al., 1992), *Reinhardtius hippoglossoides* (> 30–73 mm SL; Fahay, 2007) and *Chascanopsetta lugubris*, which may have the largest larvae among the flatfishes (reaching 120 mm SL or 135 mm TL; Amaoka, 1971).

Most pleuronectiforms metamorphose between 10–25 mm BL (Hensley and Ahlstrom, 1984) and most *Symphurus* whose larval stages are known also transform at < 20 mm BL. Size at metamorphosis is unknown for the majority of cynoglossid flatfishes because larvae of most species have not been identified and specimens in active transformation are rarely captured. Noteworthy is that the two larvae examined in this study are even larger than post-metamorphic individuals of *S. callopterus*, a deep water, eastern Pacific tonguefish that undergoes transformation at relatively large sizes (> 21 mm, but < 38 mm SL; Yevseyenko, 1990). These two pre-transitional larvae are larger than some of their metamorphosed juvenile conspecifics, and such size differentials are also observed in other flatfishes (Colton, 1961; Amaoka, 1971; Markle et al., 1992).

Possibly, large size of the pre-transitional larvae in the present study resulted from different causes. Generally, large pleuronectiform larvae (> 30 up to 70–120 mm SL) are taken in the pelagic zone over deep waters (see summary in Amaoka, 1971) and are either larvae of deep water species inhabiting the continental shelf and upper continental slope (Bruun, 1937; Amaoka, 1971; Pearcy et al., 1977; Markle et al., 1992; Minami and Tanaka, 1992; Bailey et al., 2008), or are larvae of coastal species expatriated from coastal spawning grounds that have grown to large size through delayed metamorphosis (Colton, 1961; Topp and Hoff, 1972). Kyle (1913) long ago recognized that larval size in flatfishes does not correlate with adult size of the species, but often correlates with depth of occurrence where adult populations reside. For example, he observed that deep water species of *Arnoglossus* Bleeker, 1862 and *Pleuronectes* Linnaeus, 1758 have larger larvae than do their shallow water congeners. Subsequent observations (Minami and Tanaka, 1992; Bailey et al., 2005) also support the obser-

vation that, in general, deep water flatfishes tend to have larger larvae than those of their shallow water counterparts.

Some flatfishes may also have an indefinitely prolonged postlarval stage, such as occurs in the bothid genus, *Bothus*, whose juveniles and adults may also exist pelagically (Kyle, 1913). Other larvae, such as those of the deep water pleuronectid, *M. pacificus*, are long-lived and spend a minimum of about 9 mo in the plankton, while the maximum may be over 2 yrs (Markle et al., 1992; Butler et al., 1996). Larvae with long planktonic lives are more variable in size at settling (Minami and Tanaka, 1992). Kyle (1913) noted that for some shallow water species which live contiguous to deep water, a longer pelagic existence would be adaptive in allowing larvae and pelagic juveniles and adults greater opportunity to encounter an appropriate substratum for facultative settlement into shallow water nurseries (see also Tanaka et al., 1989; Bailey et al., 2005; Abookire and Bailey, 2007 for discussion of facultative settling). Of 76 species of *Symphurus*, at least 37 are known to occur in depths > 200 m (T. Munroe, unpubl. data), but larval stages are unknown for most, rendering it difficult to determine how strong a relationship (if any) exists between larval size and depth of occurrence of adults. Among seven eastern Pacific *Symphurus* whose adults occur over a wide depth range, a relationship between larval size and depth of occurrence of adults was found (Saldierna et al., 2005), with the largest larva (25.4 mm SL) being that of the deepest occurring species, *S. callopterus*. In other oceans, larval information is available for only a few deep water *Symphurus*, and for these, size at transformation also appears larger than that for shallower-occurring species. For instance, *Symphurus ligulatus*, a deep water (205–1020 m) eastern Atlantic species (Munroe, 1990), undergoes transformation at 29 mm and smaller (Bini, 1968), and larval *S. nigrescens* (also a deep dwelling species) are 18–24 mm SL (Kyle, 1913), whereas the majority of shallow water species undergo transformation at about 20 mm SL. Because only a single larva is available for *S. varius*, it is unknown whether its large size is typical, and it would be premature to draw conclusions about larval size and depth of occurrence of adults in this species.

A variety of factors influence, and several mechanisms are employed by, different flatfish species for reaching their juvenile habitats (Able and Fahay, 1998; Burke et al., 1998; Neuman and Able, 1998; Bailey et al., 2005, 2008). Kyle (1913) found that among flatfishes inhabiting the Mediterranean Sea, larval size corresponded to life histories of the species, with shallow water species tending towards small larvae with very short pelagic phases (and restricted dispersal), while deep water species have larger larvae and relatively longer pelagic phases (with wide dispersal). Others (Minami and Tanaka, 1992; Bailey et al., 2005) have also observed that, in general, larvae of deeper dwelling flatfish species have a longer pelagic life and a larger size at metamorphosis. Bruun (1937) suggested that large larvae in deep water flatfishes is a consequence of their long pelagic life, which aids in dispersal of the individuals. Conversely, Moser (1981) offered the alternative hypothesis that large larval body size is adaptive for facilitating the larva's settling into deepwater benthic habitats, with wide dispersal being a secondary consequence. Of interest is that the deepwater bothid, *C. lugubris*, whose larvae are among the largest (to 120 mm SL) of the flatfishes, also has one of the widest distributions among the Pleuronectiformes extending throughout tropical Indo-Pacific and Atlantic oceans (Bruun, 1937; Amaoka, 1971). In contrast to the wide distribution noted for *C. lugubris*, adults and juveniles of *S. varius*, though found in relatively deep waters (78–278 m), have a much smaller geographic distri-

bution with occurrence recorded only at a few small, remote islands in the eastern Pacific Ocean surrounded by even deeper oceanic waters. For flatfishes inhabiting such areas, perhaps a large larva with a long pelagic life would be advantageous by providing flexibility in settlement opportunities or by improving chances for facultative settlement by the larva when a suitable substratum is encountered in such an expansive body of water. This would be especially true if the preferred substratum is patchily distributed and limited in extent, which very well could be the situation at these relatively small oceanic islands.

Despite its earlier developmental stage, at 36.6 mm SL, the pre-transitional larva of *S. melanurus* is more than double the size (14.5–16.7 mm SL) of four transforming individuals of *S. melanurus* collected off Colombia (Beltrán-León and Rios-Herrera, 2000). Possible explanations for this size difference are that the specimens examined by Beltrán-León and Rios-Herrera were misidentified, that considerable variation occurs in size at metamorphosis across the geographic range of this species, that standard length decreases considerably at or after metamorphosis, or as we suspect, that metamorphosis was delayed in this specimen. Since adult and juvenile *S. melanurus* reside in relatively shallow coastal seas off the west coast of the Americas, occurrence of a larva well offshore of continental areas, combined with its large size relative to that of similar species (*S. elongatus* and *S. chabanaudi*) at a comparable developmental stage, suggest this is an expatriated individual transported into deep oceanic waters probably well beyond typical settlement areas for the species.

Our knowledge of the ontogeny of species of *Symphurus* is based on relatively few specimens and more work is needed to adequately distinguish these species throughout their entire larval development. Capture of additional larval *S. varius* and *S. melanurus* will determine whether large larvae are typical for these species, or alternatively, whether such large pre-transitional larva are extraordinary individuals in delayed metamorphosis because they were expatriated from typical settlement areas for their species.

ACKNOWLEDGMENTS

We extend our appreciation to G. Aceves-Medina for providing an ontogenetic series of specimens of *Symphurus atramentatus*. H. Walker and R. Rosenblatt assisted with loan of the SIO specimen. J. Lyczkowski-Shultz provided useful information regarding terminology of larval structures. S. Raredon and L. Willis assisted with digital radiographs. L. Willis provided technical support with care of specimens. T. Munroe extends his appreciation to those curators and collection managers who supplied specimens from which comparative data were used to help identify the larvae examined in this study. The authors extend their appreciation to three anonymous reviewers whose comments and suggestions improved an earlier draft of this paper.

LITERATURE CITED

- Able, K. W. and M. P. Fahay. 1998. The first year in the life of estuarine fishes in the Middle Atlantic Bight. Rutgers Univ. Press, New Brunswick. 342 p.
- Abookire, A. A. and K. M. Bailey. 2007. The distribution and life cycle stages of two deep-water pleuronectids, Dover sole (*Microstomus pacificus*) and rex sole (*Glyptocephalus zachirus*), at the northern extent of their range in the Gulf of Alaska. J. Sea Res. 57: 198–208.

- Aceves-Medina, G., E. A. 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. 1971. Kinds and abundance of fish larvae in the eastern Tropical Pacific, based on collections made on EASTROPAC I. *Fish. Bull.* 69: 3–77.
- _____, K. Amaoka, D. A. Hensley, H. G. Moser, and B. Y. Sumida. 1984. Pleuronectiformes: development. Pages 640–670 in H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, and S. L. Richardson, eds. *Ontogeny and systematics of fishes*. Am. Soc. Ichthyol. Herpetol. Spec. Pub. 1. Lawrence.
- Amaoka, K. 1971. Studies on the larvae and juveniles of the sinistral flounders-II. *Chascanopsetta lugubris*. *Jap. J. Ichthyol.* 18: 25–32.
- Bailey, K. M., H. Nakata, and H. W. Van der Veer. 2005. Chapter 5. The planktonic stages of flatfishes: physical and biological interactions in transport processes. Pages 94–119 in R. N. Gibson, ed. *Flatfishes: biology and exploitation*. Blackwell Publ., Oxford.
- _____, A. A. Abookire, and J. T. Duffy-Anderson. 2008. Ocean transport paths for the early life history stages of offshore-spawning flatfishes: a case study in the Gulf of Alaska. *Fish. Fish.* 9: 44–66.
- Beltrán-León, B. S. and R. Rios-Herrera. 2000. Tomo 2. Estadios Tempranos de Peces del Pacifico Colombiano. Instituto Nacional de Pesca y Acuicultura. Buenaventura, Colombia. 727 p.
- Bini, G. 1968. Pleuronettiformi, Echeneiformi, Gobioesociformi, Tetraodontiformi, Lofiformi. *Atlante dei pesci delle coste italiane (1967-72)*. Mondo Sommerso, Milano, 9, Vol. 8, 164 p.
- Bruun, A. F. 1937. *Chascanopsetta* in the Atlantic; a bathypelagic occurrence of a flat-fish with remarks on distribution and development of certain other forms. *Vidensk. Medd. Dansk naturh. Foren. Kbhvn.* 101: 125–135.
- Burke, J. S., U. Masahiro, Y. Tanaka, H. Walsh, T. Maeda, I. Kinoshita, T. Seikai, D. E. Hoss, and M. Tanaka. 1998. The influence of environmental factors on early life history patterns of flounders. *J. Sea Res.* 40: 19–32.
- Butler, J. L., K. A. Dahlin, and G. Moser. 1996. Growth and duration of the planktonic phase and a stage based population matrix of Dover Sole, *Microstomus pacificus*. *Bull. Mar. Sci.* 58: 29–43.
- Chapleau, F. 1988. Comparative osteology and intergeneric relationships of the tongue soles (Pisces: Pleuronectiformes: Cynoglossidae). *Can. J. Zool.* 66: 1214–1232.
- Charter, S. R. and H. G. Moser. 1996. Cynoglossidae: tonguefishes. Pages 1408–1413 in H. G. Moser, ed. *The early stages of fishes in the California current region*. CalCOFI Atlas 33. Allen Press, Inc., Lawrence.
- Colton, J. B., Jr. 1961. The distribution of eyed flounder and lanternfish larvae in the Georges Bank area. *Copeia* 1961: 274–279.
- Emery, C. 1879. Contribuzioni all' Ittiologia. Mittheilungen aus der Zoologischen Station zu Neapel zugleich ein Repertorium für Mittelmeerkunde. 1: 581–589.
- Eschmeyer, W. N. and R. Fricke (eds.). 2009. The catalog of fishes electronic version. Updated 13 March 2009. California Academy of Sciences, San Francisco. Available from: <http://research.calacademy.org/ichthyology/catalog/fishcatsearch.html>. Accessed 18 May 2009.
- Evseenko, S. A. 2008. Early life history stages of Peacock Flounder *Bothus lunatus* (Bothidae) from the Western and Central Tropical Atlantic. *J. Ichthyol.* 48: 515–524. (Originally published (2008) in *Voprosy Ikhtiologii* 48: 517–527.)
- _____, and M. I. Shtaut. 2000. Early stages of development of two species of tongue soles-*Symphurus chabanaudi* and *S. prolatinaris* (Cynoglossidae, Pleuronectiformes) from Central Eastern Pacific. *J. Ichthyol.* 40: 751–761. (Originally published (2000) in *Voprosy Ikhtiologii* 40: 792–803.)
- Fahay, M. P. 2007. Pleuronectiformes. Pages 1496–1557 in *Early stages of fishes in the western North Atlantic Ocean (Davis Strait, Southern Greenland and Flemish Cap to Cape Hatteras)*. Vol. Two. Scorpaeniformes through Tetraodontiformes. Northwest Atlantic Fisheries Organization, Dartmouth.

- Farooqi, T. W., R. F. Shaw, J. G. Ditty, and J. Lyczkowski-Shultz. 2006. Chapter 207: Cynoglossidae. Pages 2367–2380 in W. J. Richards, ed. Early stages of Atlantic fishes: An identification guide for the Western Central North Atlantic. Vol. II. CRC Press, Boca Raton.
- Fraser, T. H. and M. M. Smith. 1974. An exterilium larval fish from South Africa with comments on its classification. *Copeia* 1974: 886–892.
- Garman, S. 1899. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galápagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer “ALBATROSS,” during 1891, Lieut. Commander Z.L. Tanner, U.S.N., commanding. 26. The fishes. *Mem. Mus. Comp. Zool. Harv. Univ.* 24: 1–431.
- Grove, J. S. and R. J. Lavenberg. 1997. Fishes of the Galápagos Islands. Stanford Univ. Press, Stanford. 863 p.
- Hensley, D. A. and E. H. Ahlstrom. 1984. Pleuronectiformes: relationships. Pages 640–670 in H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, and S. L. Richardson, eds. Ontogeny and systematics of fishes. *Am. Soc. Ichthyol. Herpetol. Spec. Pub.* 1. Lawrence.
- Kaga, T. and K. Amaoka. 2003. A postlarva of *Laeops nigromaculatus* (Bothidae: Pleuronectiformes) collected off Shirahama, Wakayama Prefecture, southern Japan. *Jap. J. Ichthyol.* 50: 131–135. (In Japanese).
- Kendall, W. C. and L. Radcliffe. 1912. Reports on the scientific results of the expedition to the eastern tropical Pacific. Pt. XXV. The shore fishes. *Mem. Mus. Comp. Zool. Harv. Univ.* 35: 72–172.
- Kramer, S. H. 1991. The shallow-water flatfishes of San Diego County. *CalCOFI Rep.* 32: 128–142.
- Kurtz, F. W. and Y. Matsuura. 1994. Early development of four tonguefishes of the Genus *Symphurus* (Osteichthyes: Cynoglossidae) from the Southern Brazil. *Jap. J. Ichthyol.* 41: 141–148.
- Kyle, H. M. 1913. Flat-fishes (Heterosomata). Pages 1–150 in Report on the Danish oceanographical expeditions 1908–1910 to the Mediterranean and adjacent seas. Vol. II. Biology. A, 1–4. Pisces.
- Leviton, A. E., R. H. Gibbs, Jr., E. Heal, and C. E. Dawson. 1985. Standards in herpetology and ichthyology. Part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985: 802–832.
- Lyczkowski-Shultz, J. 2006. Chapter 205: Poecilopsettidae: Bigeyed flounders. Pages 2349–2355 in W. J. Richards, ed. Early stages of Atlantic Fishes: An identification guide for the Western Central North Atlantic. Vol. II. CRC Press, Boca Raton.
- Mahadeva, M. N. and T. A. Munroe. 1990. Three new species of symphurine tonguefishes from tropical and warm temperate waters of the eastern Pacific (*Symphurus*: Cynoglossidae: Pleuronectiformes). *Proc. Biol. Soc. Wash.* 103: 931–954.
- Markle, D. F., P. M. Harris, and C. L. Toole. 1992. Metamorphosis and an overview of early-life-history stages in Dover sole *Microstomus pacificus*. *Fish. Bull.* 90: 285–301.
- Matarese, A. C., A. W. Kendall, Jr., D. M. Blood, and B. M. Vinter. 1989. Laboratory guide to early life history stages of northeast Pacific fishes. NOAA Tech. Rep. NMFS 80, 652 p.
- Minami, T. and M. Tanaka. 1992. Life history cycles in flatfish from the northwestern Pacific, with particular reference to their early life histories. *Neth. J. Sea Res.* 29: 35–48.
- Moser, H. G. 1981. Morphological and functional aspects of marine fish larvae. Pages 89–131 in R. Lasker, ed. Marine fish larvae: morphology, ecology, and relation to fisheries. Univ. Washington Press, Seattle.
- _____. 1996. Pleuronectiformes. Pages 1323–1324 in H. G. Moser, ed. The early stages of fishes in the California Current region. *CalCOFI Atlas.* 33. Allen Press, Inc., Lawrence.
- Munroe, T. A. 1990. Eastern Atlantic tonguefishes (*Symphurus*: Cynoglossidae, Pleuronectiformes), with descriptions of two new species. *Bull. Mar. Sci.* 47: 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.
- _____. 2005. Chapter 2. Systematic diversity of the Pleuronectiformes. Pages 10–41 in R. N. Gibson, ed. *Flatfishes: biology and exploitation*. Blackwell Science Ltd., Oxford.
- _____ and J. E. McCosker. 2001. Redescription of *Symphurus diabolicus* Mahadeva and Munroe, a poorly-known, deep-sea tonguefish (Cynoglossidae: Pleuronectiformes) from the Galápagos Archipelago. *Rev. Biol. Trop.* 49(Suppl. 1): 187–198.
- _____ and D. R. Robertson. 2005. *Symphurus ocellaris*, a new shallow-water symphurine tonguefish collected off Pacific Panama (Pleuronectiformes: Cynoglossidae). *Proc. Biol. Soc. Wash.* 118: 576–581.
- _____, F. Krupp, and M. Schneider. 1995. Family Cynoglossidae. Pages 1039–1059 in W. Fischer et al., eds. *Guía FAO para la identificación de especies para los fines de la pesca. Pacífico centro-oriental*. Vol. 2. FAO, Rome.
- Neuman, M. J. and K. W. Able. 1998. Experimental evidence of sediment preference by early life history stages of windowpane (*Scopthalmus aquosus*). *J. Sea Res.* 40: 33–41.
- Olney, J. E. and G. C. Grant. 1976. Early planktonic larvae of the blackcheek tonguefish, *Symphurus plagiusa* (Pisces: Cynoglossidae), in the lower Chesapeake Bay. *Ches. Sci.* 17: 229–237.
- Pearcy, W. G., M. J. Hosie, and S. L. Richardson. 1977. Distribution and duration of pelagic life of larvae of Dover Sole, *Microstomus pacificus*; Rex Sole, *Glyptocephaus zachirus*; and Petrale Sole, *Eopsetta jordani*, in waters off Oregon. *Fish. Bull.* 75: 173–183.
- Saavedra-Díaz, L. M., T. A. Munroe, and A. Acero. 2003. *Symphurus hernandezii* (Pleuronectiformes: Cynoglossidae), a new deep-water tonguefish from the southern Caribbean Sea off Colombia. *Bull. Mar. Sci.* 72: 955–970.
- Saldierna, R. J., E. A. González, and G. Aceves-Medina. 2005. Larval development of *Symphurus atramentatus* (Cynoglossidae: Pleuronectiformes) from the Gulf of California. *Zootaxa* 1016: 1–14.
- Tanaka, M., T. Goto, M. Tomiyama, H. Sudo, and M. Azuma. 1989. Lunar-phased immigration and settlement of metamorphosing Japanese flounder larvae into the nearshore nursery ground. *Rapp. Proceses-Verbaux Reunions. Cons. Internatl. Explor. Mer.* 191: 303–310.
- Topp, R. W. and F. H. Hoff, Jr. 1972. Flatfishes (Pleuronectiformes). *Mem. Hourglass Cruises* 4: 1–135. *Mar. Res. Lab., Fla. Dep. Nat. Resour., St. Petersburg.*
- Yevseyenko, S. A. 1990. Unusual larvae of the marine tonguefish, *Symphurus* sp. (Cynoglossidae), from central waters of the eastern Pacific. *J. Ichthyol.* 30: 148–154. (Originally published (1990) in *Voprosy Ikhtiologii* 30: 682–686.)

DATE SUBMITTED: 20 May, 2009.

DATE ACCEPTED: 10 September, 2009.

AVAILABLE ONLINE:

ADDRESSES: (T.A.M.) *National Systematics Laboratory, NMFS/NEFSC, Smithsonian Institution, Post Office Box 37012, NHB, WC 57, MRC-153, Washington, DC 20013-7012.* (T.J.K.) *Department of Biology, Museum of Southwestern Biology, MSC 03-2020, 1 University of New Mexico, Albuquerque, New Mexico 87131.* CORRESPONDING AUTHOR: (T.A.M.) *Telephone: 202-633-1293, Fax 202-633-8848, E-mail: <munroet@si.edu>.*



Appendix 1. Binomial names, taxonomic authorities, and dates of publication for species appearing in text and tables.

Species

Symphurus atricaudus (Jordan and Gilbert, 1880)
Symphurus callopterus Munroe and Mahadeva, 1989
Symphurus elongatus (Günther, 1868)
Symphurus williamsi Jordan and Culver, 1895
Symphurus chabanaudi Mahadeva and Munroe, 1990
Symphurus gorgonae Chabanaud, 1948
Symphurus oligomerus Mahadeva and Munroe, 1990
Symphurus prolatinaris Munroe, Nizinski, and Mahadeva, 1991
Symphurus atramentatus Jordan and Bollman, 1890
Symphurus diabolicus Mahadeva and Munroe, 1990
Symphurus microlepis Garman, 1899
Symphurus melanurus Clark, 1936
Symphurus varius Garman, 1899
Symphurus undecimpterus Munroe and Nizinski, 1990
Symphurus melasmatotheca Munroe and Nizinski, 1990
Symphurus ocellaris Munroe and Robertson, 2005
Symphurus lacteus (Bonaparte, 1833)
Symphurus nigrescens Rafinesque, 1810
Symphurus ginsburgi Menezes and Benvegnú, 1976
Symphurus leei Jordan and Bollman, 1890
Symphurus ligulatus (Cocco, 1844)
Bothus lunatus (Linnaeus, 1758)
Bothus ocellatus (Agassiz, 1831)
Poecilopsetta beanii (Goode, 1881)
Glyptocephalus zachirus Lockington, 1879
Laeops nigromaculatus von Bonde, 1922
Microstomus pacificus (Lockington, 1879)
Reinhardtius hippoglossoides (Walbaum, 1792)
Chascanopsetta lugubris Alcock, 1894
