**Abstract.** – Developmental stages of pygmy poacher, *Odontopyxis trispinosa*, and blacktip poacher, *Xeneretmus latifrons*, are described and illustrated from specimens collected from the northeastern Pacific Ocean. External morphology, pigmentation, and meristic features are described which distinguish larvae of these species from other agonids occurring in these waters.

Postanal pigment patterns, particularly on the caudal finfold, distinguish preflexion larvae. Odontopyxis trispinosa larvae possess a semicircular patch of melanophores that covers nearly the entire caudal finfold. The caudal finfold of preflexion X. latifrons larvae are void of pigment with the exception of a small patch of melanophores near the ventral margin of the notochord tip. Flexion and postflexion larvae can be distinguished by caudal and anal fin pigmentation, head spination, and adult meristic features.

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# Development of larval and early juvenile pygmy poacher, *Odontopyxis trispinosa,* and blacktip poacher, *Xeneretmus latifrons* (Scorpaeniformes: Agonidae)

## Morgan S. Busby

Resource Assessment and Conservation Engineering Division Alaska Fisheries Science Center National Marine Fisheries Service, NOAA 7600 Sand Point Way NE, Seattle, Washington 98115-0070

## David A. Ambrose

Southwest Fisheries Science Center National Marine Fisheries Service, NOAA P.O. Box 271, La Jolla, California 92038

The family Agonidae is a morphologically diverse group of relatively small, benthic marine fishes. Agonids, commonly called poachers, are characterized by the presence of fused or overlapping bony plates that encase the body. Fifteen genera represented by 25 species occur in the northeastern Pacific (Matarese et al., 1989).

The pygmy poacher Odontopyxis trispinosa is a small (to 8.1 cm SL) subtidal agonid distinguished by an elongate body, small vertical spine at the snout tip, and a moderately developed occipital pit divided by a longitudinal ridge. Fin-element counts of O. trispinosa are D III-VI, 5-7; A 5-7; P 13-15; V I,2 (Matarese et al., 1989). The blacktip poacher Xeneretmus latifrons is a larger (to 19 cm SL) subtidal agonid distinguished by black margins on the dorsal fins and a weakly developed occipital depression (Miller and Lea, 1972; Hart, 1973). Fin-element counts of X. latifrons are D VI-VIII, 6-8; A 6-9; P 13-15; V I,2 (Matarese et al., 1989). The presence of spiny scales on the eyeballs distinguishes X. latifrons from X. leiops. The absence of cheekplates distinguishes X. latifrons from X. triacanthus (Miller and Lea, 1972; Eschmeyer et al., 1983).

Freeman (1951) hypothesized that these two taxa are closely related phylogenetically and placed them in his subfamily Xeneretminae. The cladistic analysis of Kanayama (1991) demonstrated close relationships between the two taxa which he placed in the subfamily Anoplagoninae.

The geographic range of adult O. trispinosa extends from Southeast Alaska to central Baja California. Adult X. latifrons occur over a slightly narrower range from Vancouver Island to northern Baja California (Eschmeyer et al., 1983). Both taxa occur at depths of 18–370 m (Miller and Lea, 1972; Hart, 1973). Larval O. trispinosa and X. latifrons are the most commonly occurring agonids in the California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton collection<sup>1</sup>.

<sup>&</sup>lt;sup>1</sup>Moser, H. G., ed. Guide to the early stages of fishes from the California Current region. Southwest Fisheries Science Center, NMFS, P.O. Box 271, La Jolla, CA 92038. In preparation.

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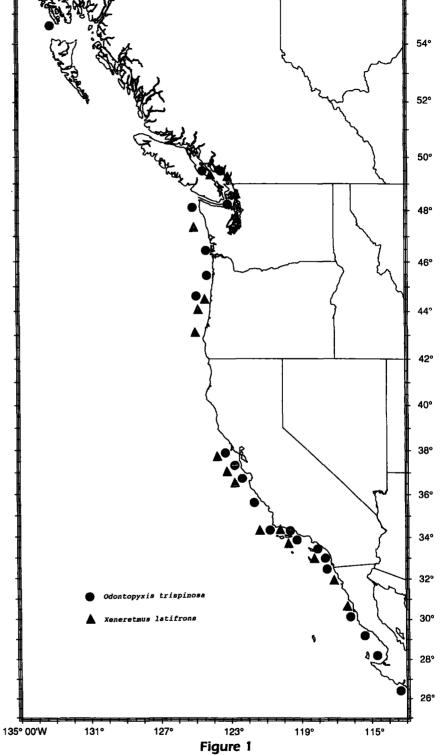
Larval development of agonids is poorly known. Washington et al. (1984) and Maeda and Amaoka (1988) reported that formation of most external body parts, including dermal bony plates and spines, begins early in larval development.

Development of the pygmy poacher (O. trispinosa) is described for the first time here. Development of X. latifrons is clarified based on new material. A partial developmental series (7, 10, 16 mm SL) of X. latifrons was previously described by Marliave (1975). Washington et al. (1984) included a single illustration of X. latifrons (9.6 mm SL) which differed markedly in appearance from those in Marliave (1975). Matarese et al. (1989) combined the illustrations from both sources to create a complete developmental series. As a result, some confusion exists as to which illustrations in this series are actually those of X. latifrons larvae. The following descriptions are the first complete accounts of larval development in the family Agonidae. Characters are presented that permit identification of these larvae from field collections.

## Methods

## **Specimens**

Agonid larvae examined in this study were obtained from collections made off the coasts of Baja California, California, Oregon, Washington (including Puget Sound), Southeast Alaska, and the inside passage waters of British Columbia, Canada (Fig. 1). One hundred and thirty-six *O. trispinosa* (4.3–56.0 mm SL) and 77 *X. latifrons* (4.8–79.0 mm SL) were examined. The largest



Collection locations of Odontopyxis trispinosa and Xeneretmus latifrons larvae and early juveniles used in this study.

specimens of each taxa were determined to be adults and are not included in the descriptions. Larvae and juveniles of both taxa were collected with dipnets, 60and 70-cm bongo nets, Isaacs-Kidd midwater trawls, Tucker trawls, sled trawls, and bottom trawls. Collections were made by the Vancouver Public Aquarium (VPA), Oregon State University (OSU), University of Washington (UW), NOAA's Southwest Fisheries Science Center (SWFSC-CalCOFI program), and the Alaska Fisheries Science Center (AFSC) from the years 1932 to 1991. Specimens are currently housed in the larval fish collections of these institutions. Larvae and juveniles were originally fixed in 3.5 or 5.0% formalin and subsequently transferred and stored in 3.5% buffered formalin or 70% ethanol.

Larvae of O. trispinosa and X. latifrons were identified using the serial approach. This method uses adult characters to progressively link juveniles to smaller specimens through a continuous sequence of shared similarities. Pigmentation, head spination, body morphology, dermal plates, and meristic features were all used as diagnostic characters. Identification of adult and juvenile specimens was accomplished by using methods of Miller and Lea (1972), Hart (1973), and Kanayama (1991). Nomenclature and taxonomic classification of the family Agonidae follow Kanayama (1991). Developmental series were illustrated by using a camera lucida attached to a dissecting stereomicroscope.

Only melanistic pigmentation is described because formalin fails to preserve color pigments. In the description of pigmentation, the term "band" refers to any aggregation of melanophores that approximates a vertically oriented rectangle. A "bar" also approximates a rectangle but is horizontally oriented. A "patch" is any other distinguishable aggregation of melanophores.

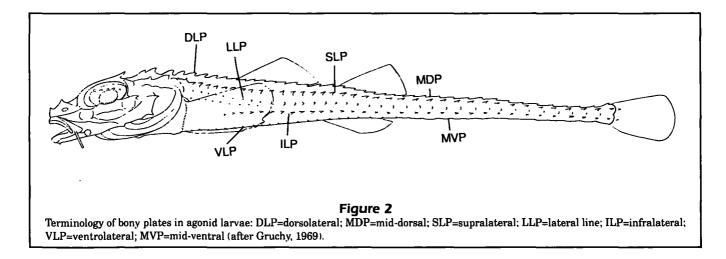
#### Measurements

The following measurements were made on 45 larvae and early juveniles of *O. trispinosa* and 45 larvae of *X. latifrons* by using an ocular micrometer in a stereomicroscope:

- **Standard length (SL)**—Snout tip to notochord tip prior to development of caudal fin, then to posterior margin of hypural element. (All body lengths in this study are standard lengths.)
- **Body depth**—Vertical distance from dorsal to ventral body margin at pectoral-fin base.
- **Snout to anus length**—Distance along body midline from snout tip to a vertical line through center of anal opening.
- **Head length (HL)**—Snout tip to posterior edge of opercle (to pectoral-fin base in small larvae before opercular margin is visible).
- **Head width**—Distance across head between dorsal margins of orbits.
- **Snout length**—Snout tip to anterior margin of orbit of left eye.
- Eye diameter—Greatest diameter of left orbit.
- **Pectoral fin length**—Distance from pectoral-fin base to tip of the longest ray.

## Osteology

Selected specimens were cleared and differentially stained to identify cartilage and bone with alcian blue and alizarin red-S (Pothoff, 1984). Skeletal elements and dermal plates were recognized as ossified upon initial uptake of alizarin red-S. Twenty-seven O. trispinosa (5.3-41 mm) and 12 X. latifrons (7.4-39.2 mm) were cleared and stained for study. Counts of meristic features were made on stained specimens only. Not all stages of development were stained for X. latifrons because specimens were limited. Preflexion, flexion, and postflexion stage larvae were stained (Kendall et al., 1984). Nomenclature of skeletal elements follows that used by Leipertz (1985) for X. triacanthus. Plate nomenclature follows that of Gruchy (1969) and is described in Figure 2. Terminology of larval head spination follows that proposed for adult



agonids by Laroche (1986). For larvae with spines and no named analogous adult spine, terminology follows Moser and Ahlstrom (1978) or Richardson and Laroche (1979) for larvae of rockfish *Sebastes* spp. (another Scorpaeniform) (Table 1, Figs. 3 and 4).

## Results

## Development of Odontopyxis trispinoa

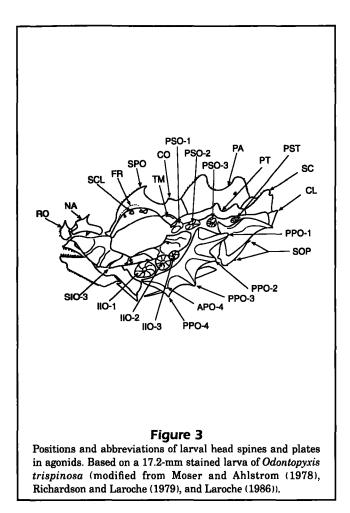
Morphology Larvae of O. trispinosa are elongate and slender with mean body depth at the pectoral fin origin of 11.7% SL in preflexion specimens decreasing to 10.7% SL in flexion and postflexion larvae (Tables 2 and 3). Mean head length is 18.4% SL in preflexion larvae and increases to 23.8% SL in juveniles (Table 3). Mean head width is approximately 50.0% HL throughout larval development and decreases to 37.1% HL in juveniles (Table 3). Mean snout length increases from 20.4% HL in preflexion larvae to 27.0% HL in postflexion larvae and eye diameter decreases from 33.3% HL in preflexion larvae to 23.3% HL in juveniles. Mean pectoral-fin length increases from 7.0% SL in preflexion larvae to 19.5% SL in postflexion larvae (Table 3). The gut is moderately long: mean snout to anus distance is 47.9% SL in preflexion larvae and decreases to 33.0% SL in juveniles.

**Pigmentation** Pigmentation in *O. trispinosa* larvae was relatively consistent among specimens and is a useful distinguishing character (Fig. 5).

**Head region** Pigmentation on the head of preflexion larvae is present as rows of melanophores on the upper and lower jaws. A few additional melanophores are present on the snout. Melanophores on the opercular and hyoid regions join the upper and lower jaw pigmentation to form a continuous swath giving larvae a "bearded" appearance (Fig. 5A). In flexion larvae, additional melanophores appear posterior to the eye.

Lateral body and gut region The dorsolateral surface of the body above the gut is covered with melanophores with the exception of a patch along the dorsal midline above the pectoral fin. The dorsolateral pigmentation recedes ventrolaterally toward the gut with development and is completely absent in postflexion larvae. Melanophores cover nearly the entire caudal portion of the body in preflexion larvae. In some specimens, the notochord tip is unpigmented. In late flexion and postflexion larvae, pigmentation on the lateral body surface begins to separate gradually into seven bands (Fig. 5D). The first band extends from the posterior region of the first dorsal fin to the ventral body midline immediately posterior to the anus. The second band extends between the first two soft rays of the

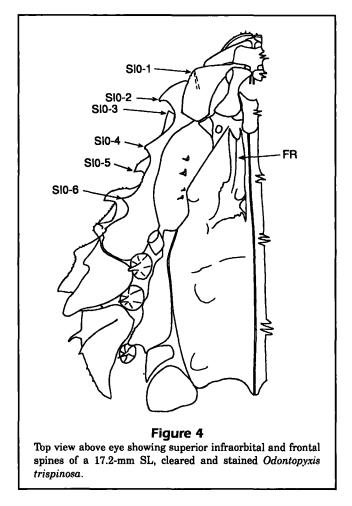
Abbreviation	Spine/Plate name	Bone of origin	Adult spine/plate
PA	Parietal	Parietal	Parietal
SPO	Supraocular	Frontal	Supraocular
SC	Supracleithral	Supracleithrum	Supracleithral
со	Coronal	Frontal	(Overgrown)
PT	Pterotic	Pterotic	Pterotic
NA	Nasal	Nasal	Nasal
APO-4	4th Anterior Preopercular	Preopercle	(Overgrown)
PPO-1,2	1st, 2nd Posterior Preopercular	Preopercle	Preopercular
PPO-3,4	3rd, 4th Posterior Preopercular	Preopercle	Preopercular
SIO-5,6	5th, 6th Superior Infraorbital	Infraorbital 3	Posterior infraorbitals
CL	Cleithral	Cleithrum	(Overgrown)
ТМ	Tympanic	Frontal	(Overgrown)
OP	Opercular	Opercle	Opercular
FR	Frontal	Frontal	(Overgrown)
SOP	Subopercular	Subopercle	Gill Cover Spine
SIO-1,2	1st, 2nd Superior Infraorbital	Infraorbital 1 (Lachrymal)	Anterior Infraorbital
PSO-1	1st Postocular	Frontal	Postocular
PSO-2,3	2nd, 3rd Postocular (P)	(Dermal)	Postocular Plates
RO	Rostral	Rostral Plate	Rostral
PST	Posttemporal (P)	(Dermal)	(Overgrown)
IIO-1,2	1st, 2nd Inferior Infraorbital (P)	(Dermal)	Anterior, Medial Cheek Plates
SIO-3,4	3rd, 4th Superior Infraorbital	Infraorbital 2 (Jugal)	Medial Infraorbital
IIO-3	3rd Inferior Infraorbital (P)	(Dermal)	Posterior Cheek Plate
SCL	Sclerotics (P)	Sclerotic	Eyeball Plates



dorsal and anal fins and is connected ventrally to the first band by a bar. The third band extends from the posterior half of the second dorsal fin to the posterior half of the anal fin. The remaining four bands are evenly spaced on the body between the posterior edges of the second dorsal and anal fins and the caudal fin. The third, fifth, and seventh bands are the widest. The posteriormost band of pigmentation in postflexion larvae and early juveniles is located at the hypural margin and is continuous with the caudal-fin pigment.

The entire ventral and lateral surfaces of the gut in preflexion larvae are covered with pigmentation. A dense row of melanophores is present along the ventral midline from the isthmus to the end of the preanal finfold. The ventral midline pigmentation can be distinguished easily in lateral view through the postflexion stage. In some specimens, a small, circular, unpigmented area is present on the lateral surface of the gut posterior to the pectoral-fin rays.

**Fins** The base of the pectoral fin is completely covered with melanophores throughout development. Pigmentation is absent from the pectoral-fin blade, rays, and membrane.



Most preflexion and flexion specimens possess a small group of melanophores on the anterior portion of the dorsal finfold near the body margin over the gut (Fig. 5A). This patch migrates posteriorly with development and becomes the pigmentation seen on the first dorsal fin in postflexion larvae and juveniles (Fig. 5, C and D). A larger patch of melanophores is present at approximately midbody which usually extends to the dorsal edge of the finfold in preflexion larvae. This dorsal midbody patch recedes toward the body and splits into two somewhat triangular-shaped patches of pigmentation in flexion larvae. This larger patch of pigmentation is retained on the second dorsal fin in postflexion larvae and juveniles. The finfold patches roughly correspond to body bands on postflexion and juvenile specimens. Three additional triangularshaped patches of melanophores are present approximately two-thirds of the distance between the anus and notochord tip on the dorsal finfold and form a continuous region of pigment extending to the caudal finfold. The triangular-shaped patches of pigmentation separate in flexion larvae and disappear as the finfold recedes in postflexion larvae.

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Standard length	Body depth	Snout to anus length	Head length	Head width	Snout length	Eye diameter	Pectoral fin length
4.3	0.44	2.02	0.78	0.40	0.14	0.28	0.30
4.5	0.60	2.06	0.72	0.52	0.12	0.30	0.30
4.6	0.60	2.24	0.80	0.44	0.18	0.30	0.34
5.2	0.62	2.48	1.02	0.48	0.22	0.32	0.34
5.3	0.60	2.52	0.96	0.46	0.20	0.32	0.44
5.3	0.64	2.60	1.02	0.46	0.18	0.36	0.36
5.9	0.62	2.72	1.04	0.42	0.20	0.34	0.38
6.4	0.74	3.24	1.14	0.44	0.26	0.36	0.34
6.7	0.70	3.24	1.20	0.56	0.22	0.40	0.46
6.8	0.76	3.20	1.26	0.56	0.30	0.40	0.50

4.3	0.44	2.02	0.78	0.40	0.14	0.28	0.30
4.5	0.60	2.06	0.72	0.52	0.12	0.30	0.30
4.6	0.60	2.24	0.80	0.44	0.18	0.30	0.34
5.2	0.62	2.48	1.02	0.48	0.22	0.32	0.34
5.3	0.60	2.52	0.96	0.46	0.20	0.32	0.44
5.3	0.64	2.60	1.02	0.46	0.18	0.36	0.36
5.9	0.62	2.72	1.04	0.42	0.20	0.34	0.38
6.4	0.74	3.24	1.14	0.44	0.26	0.36	0.34
6.7	0.70	3.24	1.20	0.56	0.20	0.40	0.46
6.8	0.76	3.24	1.20	0.56	0.22	0.40	0.50
6.8	0.82	3.12	1.20	0.62	0.30	0.36	0.50
0.8 7.2	0.82	3.48	1.40	0.02	0.30	0.30	0.50
		J.40					
7.1	0.88	3.60	1.38	0.70	0.30	0.40	0.50
7.9	0.66	3.40	1.34	0.66	0.32	0.36	0.60
8.5	0.92	4.12	1.76	0.80	0.50	0.44	0.70
9.1	0.96	4.12	1.50	0.66	0.38	0.42	1.00
9.8	1.00	4.60	2.06	0.92	0.60	0.52	1.40
10.0	1.06	4.40	1.70	1.25	0.41	0.45	1.05
10.8	1.20	5.00	2.36	1.08	0.52	0.60	1.46
11.7	1.36	5.25	2.52	1.20	0.60	0.58	1.64
 11.8	1.42	 5.50	2.26	1.24	0.74	0.56	2.46
11.8	1.44	5.42	2.20	1.24	0.74	0.60	2.46
11.8	1.44	5.42 5.67	2.80	1.24	0.78	0.60	
12.5	1.22	5.83	2.70	1.20	0.74	0.80	2.08 2.48
	1.32		2.80		0.80		2.40
12.7	1.26	5.42	2.76	1.28	0.76	0.64	2.42
12.8	1.30	5.83	2.70	1.20	0.68	0.60	2.42
13.7	1.64	6.33	2.92	1.50	0.90	0.72	2.24
13.8	1.58	6.08	2.92	1.30	0.80	0.66	2.35
13.9	1.38	6.08	3.00	1.46	0.74	0.70	2.80
14.3	1.50	6.17	3.25	1.50	0.80	0.74	2.96
14.7	1.32	5.87	3.00	1.40	0.72	0.76	2.64
14.8	1.52	6.08	3.00	1.40	0.76	0.66	2.68
15.0	1.60	5.83	3.60	1.54	0.90	0.84	3.20
15.2	1.70	5.92	3.84	1.80	1.00	0.84	3.20
15.4	1.66	6.17	3.20	1.60	0.84	0.72	3.20
15.8	1.62	6.63	3.50	1.82	0.91	0.86	3.16
16.7	1.70	6.50	4.24	2.04	1.12	0.98	3.68
17.5	1.87	6.84	4.26	1.98	1.13	0.90	3.08
17.7	2.20	7.58	4.32	1.86	1.24	0.84	3.72
17.7	1.76	7.00	4.48	2.00	1.20	1.06	3.68
28.0	2.75	9.58	7.40	2.88	1.56	1.64	4.68
32.1	3.33	10.50	7.58	2.88	1.84	1.75	5.58
34.8	3.42	11.30	8.08	3.12	1.92	2.00	6.00
36.4	3.92	11.70	8.25	2.92	2.17	1.92	6.33
41.6	4.83	14.50	9.67	3.33	2.50	2.25	6.92

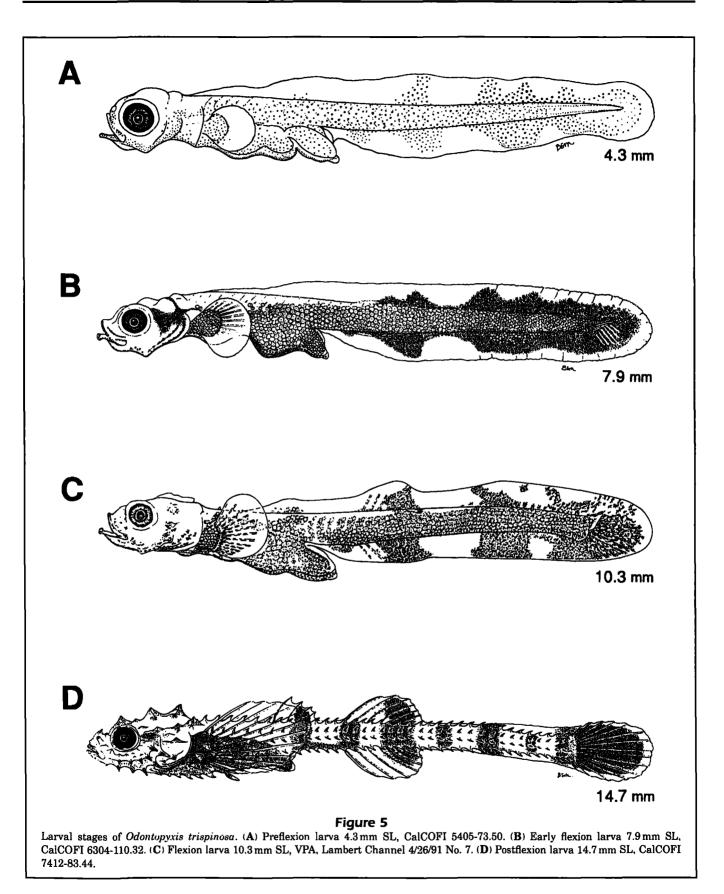
patch of melanoresent on the anal diately posterior to his small patch of n is a useful charh persists until hen it migrates dorhe receding finfold ar between the first ody bands (Fig. 5D). gular-shaped patch present at midbody nearly to the finfold margin in preflexion and early flexion larvae. The large triangular-shaped patch expands ventrally to the finfold margin and becomes more rectangular shaped in late flexion larvae. This is the only pigmentation present on the anal fin in postflexion larvae and juveniles (Fig. 5, C and D). Two additional patches of melanophores are present on the anal finfold in preflexion larvae. These form a nearly continuous region of pigmentation which begins at approximately two-thirds of the distance between the anus and notochord tip which extends to the caudal finfold. This pigmentation breaks apart in late flexion larvae and disappears as the finfold recedes in postflexion larvae.

The posteriormost dorsal and anal finfold pigmentation connect and are continuous with a large semicircular patch of melanophores which covers nearly

#### Table 3

Body proportions of Odontopyxis trispinosa larvae and early juveniles. Values given for each body proportion are expressed as percentage of standard length (SL) or head length (HL): mean, standard deviation, and range.

Body proportion	Pr	eflexion	F	lexion	Po	stflexion	Juvenile		
Sample size	12		8		20		5		
Standard length	5.7±1.0	(4.3 - 7.2)	9.4±1.5	(7.1 - 11.7)	14.5±1.9	(11.8 - 17.7)	34.6±5.1	(28.0 - 41.6)	
Body depth/SL	11.7±1.0	(10.2 - 13.4)	10.7±1.2	(8.4–12.4)	10.7±0.9	(9.0 - 12.4)	10.5±0.7	(9.8–11.6)	
Snout to anus length/SL	47.9±1.4	(45.7–50.3)	46.2±2.5	(43.2–50.8)	42.5±2.8	(38.9-46.6)	33.3±1.2	(32.1-34.9)	
Head length/SL	18.4±1.2	(16.1-20.5)	19.4±2.2	(16.5 - 21.8)	22.4±1.9	(19.2 - 25.4)	23.8±1.5	(22.7 - 26.4)	
Head width/HL	48.7±8.7	(40.4 - 72.2)	50.1±9.7	(44.0–73.5)	47.2±3.3	(43.1-54.9)	37.1±2.0	(34.4-38.9)	
Snout length/HL	20.4±2.3	(16.7 - 23.8)	24.8±2.7	(21.7 - 29.1)	27.0±2.3	(24.0-32.7)	$24.3 \pm 2.1$	(21.1 - 26.3)	
Eye diameter/HL	33.3±4.0	(25.7 - 41.7)	26.1±1.9	(23.0-29.0)	23.0±1.5	(19.4-25.3)	23.3±0.9	(22.2-24.8)	
Pectoral fin length/SL	7.0±0.7	(5.3-8.4)	10.8±2.9	(7.1 - 14.2)	19.5±1.7	(16.3 - 21.3)	17.1±0.4	(16.6-17.4)	



the entire caudal finfold. Caudal pigmentation persists throughout development.

**Osteology** Although precursors of some bony structures such as dermal plates and fin rays are discernable as early as 8.0 mm, actual ossification of skeletal elements in *O. trispinosa* does not begin until approximately 12.0 mm.

**Cranium** The parasphenoid and basioccipital bones of the cranium begin to ossify at 11.7 mm. At 13.2 mm, several bones, including the nasal, frontal, parietal, parasphenoid, basioccipital, and exoccipital are completely ossified. The rostral plate, nasal, lateral ethmoid, supraethmoid, vomer, exoccipital, lachrymal, and remainder of the circumorbital series ossify by 14.8 mm. The sphenotic, prootic, epiotic, tabular, and pterosphenoid are ossified by 27.0 mm.

**Spines** Numerous head spines are ossified at 12.6 mm including the nasal, supraocular, the large bilobed parietal, coronal, pterotics, supracleithral, anterior preoperculars and posterior preoperculars 1 and 2. The tympanic, cleithral, opercular, fifth and sixth superior infraorbital spines, and the third and fourth posterior preopercular spines are also ossified at this stage. The frontal spine forms by 13.8 mm but is not visible in lateral view because it is small and located behind the anterior margin of the supraocular spine. The frontal spine becomes overgrown with bone and is difficult to distinguish at 17.2 mm. Interopercular and superior infraorbital spines 1 and 2 begin forming at about 14.2 mm. The rostral and postocular spines and the postocular and posttemporal plates ossify at 14.8 mm. Superior infraorbital spines 3 and 4 and inferior infraorbital plates 1 and 2 are completely ossified at this size. The third inferior infraorbital and sclerotic plates are ossified by 17.2 mm. All spines described here are paired with the exception of the rostral.

Mandibular region The dentary, angular, and articular bones of the lower jaw are the first to ossify in postflexion larvae of 11.7 mm. At 12.6 mm, the premaxilla and maxilla are ossified.

**Palatine region** Palatine, quadrate, metapterygoid, mesopterygoid, ectopterygoid, and symplectic bones are ossified at 12.6 mm.

**Opercular region** The preopercle, opercle, interopercle, and subopercle are ossified by 12.6 mm.

**Hyoid region** The basihyal, hypohyal, urohyal, ceratohyal, epihyal, interhyal, glossohyal, and branchiostegal rays are also ossified by 12.6 mm. The hyomandibula is ossified by 27.0 mm.

**Branchial region** The pharyngobranchial teeth are the first structures to ossify by 11.7 mm. Ossification of the pharyngobranchials occurs at about 17.2 mm. The pharyngobranchials begin as four pieces of cartilage that apparently fuse before ossification of the pharyngobranchial teeth. This process, however, was not observed. The epibranchials (n=4) and ceratobranchials (n=5) also ossify by 17.2 mm. The remaining branchial support structures, including the hypobranchials (n=3) and basibranchials (n=3), ossify by 27.0 mm.

Appendicular region The cleithrum, postcleithrum, and coracoid are ossified by 12.6 mm. The pelvic-fin spine and all pectoral-fin rays, with the exception of the ventralmost, ossify by 12.8 mm. The two pelvic-fin rays and the final (14th) pectoral-fin ray are ossified by 13.2 mm. The supracleithrum ossifies at about 13.8 mm. At 14.8 mm, ossification of the posttemporal is completed. Ossification of the basipterygium occurs at 17.2 mm. The scapula and three radials supporting the pectoral-fin rays are ossified by 27.0 mm.

Median fins All dorsal- and anal-fin spines and soft rays are ossified by 12.6 mm (Table 4). Six superior principal rays and five inferior principal rays in the caudal fin are ossified at this size (total=11). One inferior principal (12), and two superior procurrent rays (13, 14) are ossified by 13.2 mm. By 17.2 mm one additional superior (15) procurrent caudal ray is formed which completes the adult count (3+6+6+0=15). Ossification of the epural, hypural plate, and pterygiophores supporting the dorsal- and anal-fin rays is completed by 27.0 mm.

Vertebral column Ossification of vertebral elements progresses from anterior to posterior. Notochord flexion begins at approximately 7.0 mm and is completed by 11.8 mm. All, except the posteriormost caudal vertebral centrum, are ossified by 12.6 mm. The urostyle and the anteriormost neural and haemal spines are also complete by 12.6 mm. All abdominal neural spines are complete and three additional haemal spines form anteriorly by 13.2 mm. All vertebral centra are ossified by 13.8 mm and two additional haemal spines have formed. By 14.2 mm, 22 additional haemal spines develop. All neural spines are ossified by 14.8 mm and haemal spines are complete at 15.4 mm.

**Dermal plates** Precursors of the supra (SLP) and infralateral (ILP) plates first appear as small singular spines which are distinguishable at about 8.0 mm. Ossification, however, does not begin until approximately 12.0 mm and progresses from anterior to posterior. Bone develops radially from the base of the spine to eventually form the juvenile/adult dermal plate. By 12.6 mm, ossification of the SLP and ILP series is complete. The dorsolateral and mid-dorsal (DLP+MDP) and the ventrolateral and mid-ventral (VLP+MVP) plate series are complete by 14.8 mm. The lateral line (LLP) plate series begins to form at about 14.0 mm. Lateral line plates are the only plates that begin development as bifurcate spines. Ossification of the LLP series is complete

Standard	Dorsa	l fin	A	Destand	Pelvic fin		Nei	ıral spine	S	۲۲		Centra			В	ody pla	Body plates*			
length (mm)	spines	rays	-	Pectoral fin rays	spines, rays	ostegal rays	abdominal	caudal	total	Haemal spines	abdominal	caudal	total	DLP+MDP	SLP	LLP	ILP	VLP+MVI		
5.3													-							
5.8																				
6.1																				
7.7																				
8.3																				
8.5																				
9.3																				
10.0																				
11.4																				
	• — — -																			
12.5																				
12.6	5	6	6	13	Ι	6	3		3		` 13	25	38	30	35		35	32		
13.1	3	6	2	2																
13.2	5	6	6	14	I.2	6	13	20	33	3	13	27	40	32	38	2	36	34		
13.8		3				6	2		2											
13.8	4	6	7	13	I,2	6	13	22	35	6	13	27	40	34	38		36	37		
14.2	5	7	6	14	I,2	6	13	19	32	5	13	26	39	34	36	1	35	34		
14.8	5	7	6	14	I,2	6	13	25	38	29	13	26	39	36	38	38	37	36		
15.2	5	6	6	13	I,2	6	13	25	38	23	13	26	39	37	39	33	37	37		
15.2	4	4	6	14	I,2	6	13	25	38	26	13	26	3 <del>9</del>	37	37	1	35	36		
15.4	4	6	7	14	I,2	6	13	24	37	31	13	25	38	36	37	23	36	37		
16.7	5	f	6	14	I,2	6	13	25	38	31	13	26	39	37	37	20	35	37		
17.2	6	6	7	14	I,2	6	13	25	38	31	13	26	39	37	38	38	36	37		
27.0	4	6	5	14	I,2	6	13	25	38	32	13	26	39	36	37	39	36	36		
29.0	5	6	6	14	I,2	6	13	24	37	31	13	25	38	37	39	38	36	37		
41.0	4	6	6	13	I,2	6	13	24	37	31	13	25	38	36	38	39	36	36		

by 17.2 mm. Breast plates on the ventral surface of the abdomen and pelvic region are complete by 12.6 mm. The number of pectoral-fin base plates in O. *trispinosa* is variable ranging from 3 to 8 among specimens examined. Ossification of pectoralfin base plates is complete by about 13.8 mm.

## Development of Xeneretmus latifrons

Morphology Larvae of X. latifrons are deeper bodied than O. trispinosa; mean body depth at the pectoral-fin origin ranges from 13.3% SL in preflexion specimens to 14.6% SL postflexion (Tables 5 and 6; Fig. 6). Head length increases from 20.3% SL in preflexion larvae to 26.6% SL in postflexion larvae, and snout length as a proportion of head length increases from 18.8% HL in preflexion larvae to 24.4% HL in postflexion larvae (Table 6). Eye diameter decreases from about 37.5% HL in preflexion larvae to 28.4% HL in postflexion larvae, and head width remains approximately 54-55% HL throughout development (Table 6).

Pectoral-fin length increases from 8.4% SL in preflexion larvae to 21.8% SL in postflexion larvae. In preflexion larvae, snout to anus distance is 51.7%

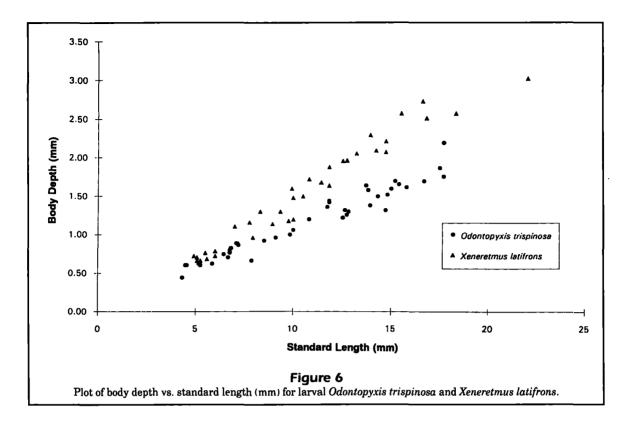
Table 5
Morphometric measurements (in millimeters) of 45 Xeneretmus latifrons larvae. Speci-
mens between dashed lines (— —) were undergoing notochord flexion.

Standard length	Body depth	Snout to anus length	Head length	Head width	Snout length	Eye diameter	Pectoral fin length
4.9	0.72	2.20	0.84	0.48	0.06	0.38	0.34
5.1	0.66	2.56	0.96	0.50	0.16	0.38	0.34
5.1	0.70	2.48	1.06	0.54	0.20	0.38	0.38
5.3	0.66	2.40	0.90	0.44	0.16	0.38	0.32
5.5	0.76	2.88	1.26	0.66	0.26	0.40	0.44
5.6	0.68	2.92	1.00	0.50	0.20	0.40	0.40
6.0	0.78	2.92	1.14	0.64	0.23	0.44	0.50
6.0	0.72	2.98	1.15	0.60	0.22	0.40	0.40
6.8	0.82	3.40	1.32	0.66	0.24	0.46	0.42
6.8	0.80	3.36	1.20	0.66	0.20	0.42	0.50
7.0	1.10	3.80	1.66	0.80	0.28	0.46	0.52
7.2	0.88	4.04	1.80	1.00	0.42	0.52	1.08
7.8	1.16	4.80	2.08	1.08	0.56	0.64	1.14
7.9	0.96	4.12	1.54	0.84	0.30	0.48	0.62
8.3	1.30	4.78	1.54	1.13	0.32	0.61	0.81
8.9	1.14	4.78	1.94	1.04	0.44	0.62	0.88
9.3	1.30	5.67	2.68	1.52	0.50	0.82	1.80
9.8	1.18	5.33	2.44	1.24	0.56	0.68	1.50
9.9	1.60	5.50	2.56	1.44	0.64	0.74	1.80
10.0	1.20	6.08	2.44	1.36	0.60	0.74	1.62
10.0	1.48	5.67	2.36	1.30	0.54	0.70	1.42
10.5	1.50	5.75	2.96	1.64	0.62	0.86	2.48
10.8	1.72	<u> </u>		1.42	0.62		2.14
10.8	1.72	6.25	2.80	1.80	0.64	0.88	2.32
11.4	1.68	6.50	2.88	1.86	0.72	0.88	2.30
11.8	1.88	6.50	2.88	1.70	0.74	0.78	2.20
11.8	1.64	6.08	2.88	1.90	0.70	0.76	3.00
12.5	1.96	6.67	3.28	1.94	0.78	1.02	2.64
12.7	1.97	7.00	3.44	1.88	0.94	0.86	2.80
12.7	1.96	6.67	3.36	2.06	0.66	0.96	3.00
13.2	2.06	6.70	3.52	2.00	0.90	0.92	3.12
13. <del>9</del>	2.30	7.08	3.92	2.30	0.98	1.02	3.52
14.2	2.10	7.12	4.04	2.10	1.10	1.08	3.72
14.7	2.22	7.58	3.84	2.12	0.94	1.02	3.52
14.7	2.08	7.33	3.56	2.10	0.78	0.96	3.76
15.5	2.58	7.14	3.80	2.58	0.91	1.09	3.73
16.6	2.74	8.06	4.86	2.30	1.06	1.22	4.40
16.8	2.52	7.92	4.60	2.40	1.16	1.26	3.84
18.3	2.58	8.06	4.86	2.74	1.37	1.22	4.10
22.0	3.04	9.40	5.17	3.04	1.67	1.52	4.41
30.0	3.67	11.50	8.67	3.60	2.25	2.25	5.33
30.5	4.00	11.30	8.67	4.33	1.92	2.92	5.50
31.8	3.92	11.80	9.58	4.42	2.00	3.08	5.58
39.2	4.33	12.70	10.70	4.75	2.33	3.42	6.83
42.0	5.12	14.20	11.20	5.42	2.50	3.67	7.08

#### Table 6

Body proportions of *Xeneretmus latifrons* larvae. Values given for each body proportion are expressed as percentage of standard length (SL) or head length (HL): mean, standard deviation, and range.

Body proportion	Pr	eflexion	F	lexion	Postflexion		
Sample size	15	_	8		22		
Standard length	6.3±1.1	(4.9-8.3)	9.9±0.6	(8.9-10.8)	19.0 <del>±9</del> .4	(10.8-42.0)	
Body depth/SL	13.3±1.4	(11.9–15.7)	14.2±1.6	(12.1 - 15.9)	14.6±1.6	(11.0-16.6)	
Snout to anus length/SL	51.7±4.5	(44.7-61.9)	56.7±2.7	(53.6-60.8)	47.4±7.6	(32.4-57.9)	
Head length/SL	20.3±3.0	(17.1 - 26.8)	25.3±2.3	(21.7 - 28.7)	26.6±1.8	(23.5-30.1)	
Head width/HL	53.9±6.0	(48.2–73.4)	54.8±2.0	(50.8-56.7)	55.6±7.2	(41.5-67.9	
Snout length/HL	18.8±4.2	(7.1 - 26.9)	22.6±2.0	(18.7–25.0)	24.4±2.8	(19.6-32.3	
Eye diameter/HL	37.5±5.1	(27.7 - 45.2)	29.8±1.2	(27.9-32.0)	28.4±2.8	(25.0-33.7	
Pectoral fin length/SL	8.4±2.8	(6.1–15.1)	17.1±4.1	(9.9–23.6)	$21.8\pm3.1$	(16.9-26.5	
•							



SL, increases to 56.7% SL during flexion, and decreases to 47.4% SL during postflexion.

**Pigmentation** Pigmentation in X. latifrons is consistent among specimens and is a useful distinguishing character (Fig. 7). Because pigmentation on the head and gut regions of X. latifrons is so similar to that described previously for O. trispinosa, discussion here will be limited to areas of the lateral body and fins that are diagnostically important.

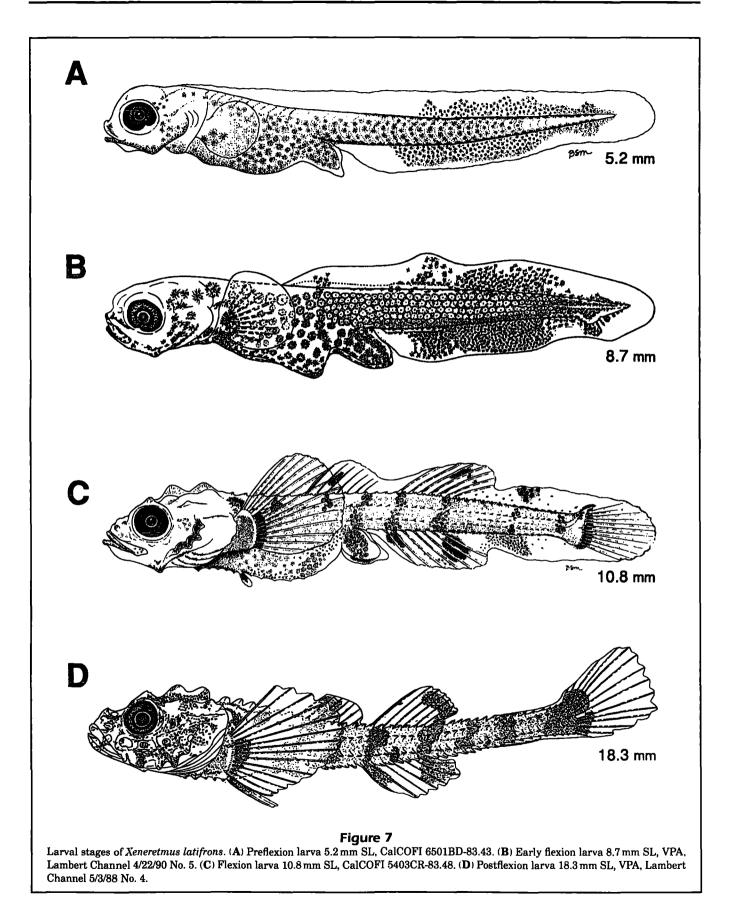
Lateral body The lateral surface of the body above the gut in preflexion larvae is covered with melanophores, with the exception of an elongate, unpigmented area along the dorsal midline above the pectoral fin. Melanophores cover nearly the entire caudal region of the body, with the exception of the notochord tip. Melanophores extend along the dorsal and ventral margins of the unpigmented area around the notochord tip (Fig. 7A). By early flexion, melanophores completely cover the notochord tip (Fig. 7B).

Three patches of melanophores appear along the dorsal midline near the notochord tip by about 10.5 mm SL (Fig. 7C). The anterior patch forms the first band which extends from the dorsal margin of the body, posterior to the pectoral-fin base, to the anterior lateral gut area. The second band extends dorsally to connect with pigmentation seen on the first dorsal fin. The third band transverses the body between the posteriormost dorsal spine and the gut. Four or five distinct bands of pigmentation form between the anterior edges of the second dorsal and anal fins and the caudal fin. The first two bands transverse the body between the anterior and posterior margins of the second dorsal and anal fins. One or two bands are present between the posteriormost dorsal- and anal-fin rays and the hypural margin. The last band is the widest and covers the hypural region, extending into the caudal fin approximately 15–20% of its length (Fig. 7, C and D).

**Fins** Melanophores begin to appear on the ventral margin of pectoral-fin base at about 5.0 mm. The pectoral-fin base is completely covered with pigment by 6.0 mm. Pigmentation is always absent from the pectoral-fin blade, rays, and membrane (Fig. 7, A and B).

A small patch of melanophores appears in the dorsal finfold above the constriction of the gut at about 6.0mm (Fig. 7B). This pigmentation later expands and is that seen on the spinous (first) dorsal fin in late flexion and postflexion larvae (Fig. 7, C and D). Posteriorly, an additional patch of pigmentation begins about one-third of the distance between the anus and notochord tip and exhibits an irregular edge, appearing somewhat serrated, below the dorsal margin.

In preflexion larvae, a large patch of melanophores covers most of the anal finfold beginning at approximately one-fourth of the distance between the anus and notochord tip and continuing its entire length. The rela-



tively large unpigmented area anterior of this patch is an important diagnostic feature (Fig. 7, A and B).

Both the dorsal and ventral finfold melanophore patches are constricted nearly to the body margins at a point about 80%-90% of the distance between the anus and notochord tip (Fig. 7B). As notochord flexion progresses, the ventral patch of pigmentation posterior to the constriction on the anal finfold is seen as the post-hypural pigment present on the caudal fin of postflexion specimens (8.7-22.0 mm)(Fig. 7C). This caudal-fin pigmentation extends posteriorly to about 15-20% of the caudal-fin length (Fig. 7, C and D).

The remaining melanophores on the dorsal and anal finfolds migrate toward the body margins as the finfold recedes. Discrete melanophore patches remain on the anterior and posterior margins of the second dorsal and anal fins in postflexion larvae (Fig. 7D).

**Osteology** Although precursors of some bony structures such as dermal plates and fin rays are discernable as early as 8.0 mm, ossification in X. latifrons does not begin until approximately 13.0 mm. The sequence of ossification of bony structures in X. latifrons is nearly identical to that described previously for O. trispinosa. The most important difference to note is that ossification in X. latifrons begins later (13.0 mm), progresses more rapidly for lateral body plates, and is slower for most skeletal elements than O. trispinosa. The intent here is to highlight important differences between the two taxa.

**Cranium** All parts of the cranium, with the exception of the sphenotic, prootic, epiotic, tabular, and pterosphenoid are ossified at 13.8 mm. These remaining cranial elements ossify at about 30.5 mm.

Mandibular region Ossification of all mandibular structures is complete at 13.8 mm.

**Spines** Head spination is generally reduced in X. latifrons larvae. Xeneretmus latifrons larvae have no inferior infraorbital, postocular, or posttemporal plates and have only four superior infraorbital spines. The rostral spine, which is weaker than that of O. trispinosa, and sclerotic plates do not develop until the late postflexion stage (about 25–30 mm). The tympanic and frontal spines are more pronounced in X. latifrons larvae than in O. trispinosa.

**Palatine region** The palatine, quadrate, metapterygoid, mesopterygoid, ectopterygoid, and symplectic are ossified at 13.8 mm.

**Opercular region** The preopercle, opercle, subopercle, and interopercle are ossified by 13.8 mm.

**Hyoid region** The basihyal, hypohyal, urohyal, ceratohyal, epihyal, interhyal, glossohyal, and branchiostegal rays are ossified by 13.8 mm. The hyomandibula is ossified at 30.5 mm.

**Branchial region** The pharyngobranchial teeth, pharyngobranchials (*n*=4, fused as in *O. trispinosa*),

ceratobranchials (n=5), and epibranchials (n=4) ossify at about 21.0 mm. The remainder of the branchial apparatus including the basibranchials (n=3) and hypobranchials (n=3), are ossified by 30.5 mm.

**Appendicular region** The cleithrum, postcleithrum, supracleithrum, and coracoid are ossified by 13.8 mm. Pelvic-fin spines and rays and all pectoral-fin rays are complete at 13.8 mm (Table 7). The basipterygium and posttemporal ossify by 21.0 mm. The scapula and three radials supporting the pectoral fin are ossified by 30.5 mm.

Median fins All dorsal-, anal-, and caudal-fin spines and soft rays are ossified by 13.8 mm (Table 7). The caudal fin has 6 superior principal, 2 superior procurrent, 6 inferior principal, and 1 inferior procurrent rays (2+6+6+1=15 total). Ossification of the hypural plate and the pterygiophores supporting the dorsaland anal-fin rays was not complete in the largest specimen examined (39.2 mm).

Vertebral column Notochord flexion begins at approximately 8.5 mm and is completed by 11.0 mm. All vertebral centra and the urostyle are ossified by 13.8 mm. All except the two posteriormost neural and three haemal spines are also ossified at 13.8 mm. Ossification of all neural and haemal spines is complete by 14.5 mm (Table 7).

**Dermal plates** All dermal plates are ossified by 13.8 mm. Sequence and direction of formation and ossification is the same as previously described for *O. trispinosa. Xeneretmus latifrons*, however, has higher DLP+MDP, ILP, and VLP+MVP lateral body plate series counts than *O. trispinosa* (Tables 4 and 7). A maximum of five pectoral-fin plates was counted in *X. latifrons*.

## Discussion

## Summary comparison of *O. trispinosa* and *X. latifrons* larvae

Larvae of O. trispinosa and X. latifrons can be distinguished by pigmentation, morphological, and meristic characters.

Larvae of O. trispinosa possess a semicircular patch of melanophores that nearly covers the entire caudal finfold. This character is diagnostic and present throughout development. The caudal finfold of preflexion X. latifrons lacks pigmentation except for a patch located near the ventral margin of the notochord tip. This patch becomes elongate as notochord flexion progresses and becomes a band at the hypural margin. This band extends onto the caudal fin and may cover as much as 20% of its anterior surface.

Preflexion larvae of *O. trispinosa* possess a small patch of melanophores on the anal finfold immediately posterior to the origin, *X. latifrons* larvae have a large

length —	Dorsal fin		ard Dorsa	A 1 C .	Destand	Pelvic fin		Neu	ıral spine	8	Haemal		Centra			В	ody pla	ates*	
	spines	rays	Anai in rays	Pectoral fin rays	spines, rays	ostegal rays	abdominal	caudal	total		abdominal	caudal	total	DLP+MDP	SLP	LLP	ILP	VLP+MVF	
7.4																			
8.7																			
9.5																			
10.2																			
11.9																			
12.3																			
13.8	7	7	7	15	I,2	6	14	25	39	33	14	28	42	38	38	38	38	38	
14.5	6	7	7	14	I,2	6	14	27	41	34	14	28	42	38	38	38	38	38	
21.0	7	6	7	14	I,2	6	15	26	41	35	15	27	42	41	41	41	40	41	
30.5	7	7	7	15	1,2	6	15	25	40	33	15	26	41	38	38	40	38	38	
31.8	7	7	7	14	I,2	6	15	25	40	34	15	26	41	38	38	42	38	38	
	6	6	7	14	I,2	6	15	26	41	34	15	26	41	38	38	40	38	38	

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unpigmented region. Flexion and postflexion larvae of O. trispinosa possess a single patch of melanophores on the anal fin, X. latifrons have two.

Notochord flexion of O. trispinosa begins at approximately 7.0mm and is completed by 11.8 mm. The largest planktonic specimens of O. trispinosa collected were 17.7 mm. Settlement probably occurs at approximately this size. Notochord flexion of X. latifrons begins at approximately 8.5 mm and is completed by 11.0 mm. The largest planktonic specimens of X. latifrons collected were 22.0 mm.

Xeneretmus latifrons larvae are deeper bodied than O. trispinosa. Xeneretmus latifrons also has a wider head than O. trispinosa at all stages of development. Single barbels are present at the corners of the mouth at about 15.0 mm in O. trispinosa and 18.0 mm in X. latifrons. A distinct heart-shaped occipital pit is present in O. trispinosa after about 15.0 mm. Post-flexion larvae of each taxon are also distinguishable by adult meristic characters.

Ossification of most skeletal elements in O. trispinosa begins earlier and is completed at smaller sizes than in X. latifrons. Head spination in X. latifrons is generally reduced and dermal plates are absent on the head region. The caudal-fin ray complement in X. latifrons (2+6+6+1) is notably different than in O. trispinosa (3+6+6+0). Ossification of the pterygiophores supporting the dorsal and anal fins, and the hypural plate is complete by 27.0 mm in O. trispinosa, but was not evident in cleared-and-stained specimens of X. latifrons examined in this study (up to 39.2 mm). This indicates that transformation from larval to juvenile stages in X. latifrons occurs at much larger sizes than in O. trispinosa. Ossification of dermal body plates occurs in nearly identical sequence, but X. latifrons has more plates in the DL+MD, IL, and VL+MV series. Dermal plate formation in X. latifrons is complete at a slightly smaller size than in O. trispinosa.

The preceding descriptions eliminate the confusion in the literature concerning these larvae which resulted from previous misidentifications (page 463 of Matarese et al. (1989) and Figures A, B, and D from Marliave (1975) are larvae of *O. trispinosa* misidentified as *X. latifrons*; Figure C from Washington et al. (1984) is *X. latifrons*).

# Comparison of *O. trispinosa* and *X. latifrons* larvae with other known larval agonids

Presently, larvae of 12 of 25 agonid taxa occurring in the northeastern Pacific Ocean can be identified based on single illustrations or complete developmental descriptions. Of these 12 taxa, only *O. trispinosa* and *X. latifrons* described here are complete, illustrated at all stages of development and include discussions of ossification sequence.

By using body morphology, pigmentation, and meristic characters, larvae of O. trispinosa and X. latifrons are distinguishable from other northeastern Pacific

	Characters										
Species	Body depth	Pectoral fin length	Pigmentation	Number of dorsal fins	Pectoral fin rays	Vertebrae					
Aspidophoroides monopterygius	Slender	Elongate	Light	1	9–10	51–53					
Bothragonus swanii	Deep	Normal	Moderate	2	10-12	29-31					
Chesnonia verrucosa	Moderate	Elongate	Light	2	14–15	3438					
Hypsagonus mozinoi	Deep	Normal	Heavy	2	11-12	34					
H. quadricornis	Deep	Normal	Heavy	2	12 - 14	36					
Leptagonus leptorhynchus	Moderate	Normal	Heavy	2	13-15	42–44					
Ocella dodecaedron	Moderate	Normal	Light	2	14-16	38–39					
Odontopyxis trispinosa	Moderate	Normal	Moderate	2	13-15	37-42					
Percis japonicus	Deep	Normal	Heavy	2	12	40,42					
Stellerina xyosterna	Moderate	Elongate	Light	2	17–19	34–37					
Ulcina olriki	Slender	Elongate	Moderate	1	13-16	38-40					
Xeneretmus latifrons	Moderate	Normal	Moderate	2	13-15	39-43					

\*Sources: Illustrations of A. monopterygius, C. verrucosa. H. quadricornis and S. xyosterna are from Washington et al. (1984); B. swanii is from Marliave (1975); H. mozinoi is from Matarese et al. (1989); L. leptorhynchus, O. dodecaedron, and P. japonicus are from Maeda and Amaoka (1988); U. olriki is from Dunbar (1947). Pectoral-fin ray and vertebral counts are from Matarese et al. (1989), with the exception of H. mozinoi and the lower count for P. japonicus which are from Kanayama (1991).

agonid larvae for which published illustrations are available. (Table 8). Larvae of Hypsagonus mozinoi, H. quadricornis, and Percis japonicus are deeper bodied, have notably shorter snout to first dorsal fin distances, are more heavily pigmented, and have lower vertebral and dermal plate counts than O. trispinosa and X. latifrons (Washington et al., 1984; Maeda and Amaoka, 1988; Matarese et al., 1989). Bothragonus swanii larvae have a very similar body morphology to H. mozinoi, H. quadricornis, and P. japonicus but have considerably less pigmentation (Marliave, 1975).

Larvae of Chesnonia verrucosa and Stellerina xyosterna have similar body morphologies to O. trispinosa and X. latifrons but have notably larger pectoral fins with bands of pigmentation on or near their posterior edges (Washington et al., 1984; Matarese et al., 1989). Ocella dodecaedron and Leptagonus leptorhynchus larvae have a similar body morphology to X. latifrons. However, pigmentation of O. dodecaedron is more sparse and that of L. leptorhynchus is heavier (Maeda and Amaoka, 1988).

Larvae of Ulcina olriki are distinguished from O. trispinosa and X. latifrons by having larger pectoral fins with pigmented edges and only a single dorsal fin (Dunbar, 1947). Larvae of Aspidophoroides monopterygius (= A. bartoni) have extremely slender bodies, a long pectoral fin with a low fin-ray count, higher vertebral and body plate counts, and a single dorsal fin (Maeda and Amaoka, 1988; Matarese et al., 1989). Studies such as this and others planned for the future are the first steps for providing diagnostic information necessary to accurately identify early life history stages of this interesting family of fishes.

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