RICHARD K. STROUD

Northwest and Alaska Fisheries Center
National Marine Fisheries Service, NOAA
7600 Sand Point Way NE., Seattle, WA 98115
Present address: *Department of Veterinary Medicine*
Oregon State University
Corvallis, OR 97331

CLIFFORD H. FISCUS
HIROSHI KAJIMURA

Northwest and Alaska Fisheries Center
National Marine Fisheries Service, NOAA
7600 Sand Point Way NE., Seattle, WA 98115

SPAWN AND LARVAE OF THE PACIFIC SANDFISH, *TRICHODON TRICHODON*

Little is known about the biology of the Pacific sandfish, *Trichodon trichodon*, other than that the adults are characteristic of inshore, sand-gravel communities (Isakson et al. 1971); they occur from San Francisco, Calif., to Kamchatka, USSR (Hart 1973); and they burrow into a sandy substrate (Clemens and Wilby 1961). Clemens and Wilby reported that a mature female taken on Long Beach, Vancouver Island, Canada, extruded mature eggs (upon disturbance) in February.

The first discovery of natural spawn of *T. trichodon* and subsequent rearing of larvae through metamorphosis at the Vancouver Public Aquarium has provided information about the reproduction and early life history of this species. In addition to life history notes, this paper presents a description of larvae of *T. trichodon*.

Methods

A portion of an egg mass was collected at lat. 48°56′ N, long. 125°43′ W, 16 km southeast of Long Beach, Vancouver Island, on 12 June 1976 and transported in a plastic bag with oxygen and seawater to the Vancouver Aquarium, where it was incubated in an aerated aquarium with seawater (25-29‰, 8°-13° C) provided at an inflow rate exceeding 100 tank volumes/d. The seawater temperature changed seasonally with changes in average ambient seawater surface temperatures, so that the salinity/temperature regime was comparable with that which the eggs would have encountered intertidally. The eggs were fixed in a bag of nylon mesh in front of the inlet pipe. In October, December, and January, embryos were excised from a few of the eggs to determine whether development was continuing. About once per month egg membranes were scrubbed with a bottle brush to remove diatom growth.

As they hatched the larvae were collected with a beaker and transferred to a 1,000 l rearing tank (ca. 1 m depth × 1 m in diameter) with seawater (25-27‰, 10°-12° C) inflow at a rate exceeding one tank volume per day and a light cycle of 14 h light and 10 h dark, including simulated twilight periods. Larvae were provided brine shrimp, *Artemia salina*, nauplii daily in excess quantities. Debris was siphoned from the tank bottom daily and examined for dead fish larvae. Juveniles were placed in a tank with a sand bottom and flow-through seawater and were fed frozen euphausiids and frozen brine shrimp.

At various ages specimens were preserved in 3% Formalin[1] in seawater, with borax and Ionol. Freshly killed specimens were measured to the nearest 0.5 mm standard length (SL), then measured again 1 yr after preservation, to determine shrinkage. Line drawings, morphometric data, and meristic characters were based on preserved specimens.

Life History Notes

The egg mass was found in a surge channel on a rocky shoreline between 0.6 and 1.0 m tide levels. The mass was visually estimated to have about 1,000 eggs, was irregularly shaped, and adhered firmly to the rock surface.

Adults of this species are known to inhabit sandy beaches, whereas the egg mass is suited only to rocky substrate to which it can adhere. Presuming an incubation period of about 1 yr as discussed below, most plant substrates would be too ephemeral for an egg deposition site and bedrock on sand beaches could be covered by seasonal shifting of sand. Rocky shoreline removed from sandy areas would therefore provide the most stable substrate for the adhesive eggs. The precise location on the wall of a fully exposed surge channel might provide a refuge from egg predation as well as high flow velocities for gas exchange. The rocky intertidal area in which this egg mass occurred is located 8 km from the nearest sandy intertidal area. Thus, a limited spawning movement along the shore must occur.

[1]Reference to trade names does not imply endorsement by the Vancouver Aquarium or by the National Marine Fisheries Service, NOAA.

The *T. trichodon* eggs were amber colored and large in size (3.52 mm in diameter ±0.10 SE, n = 17 eggs), and slightly flattened at points of attachment. About 25% of the collected eggs were dead at the time they were taken. When collected the embryos had developed both melanic choroid pigment and guanine iris pigment on the eyes.

Considering the state of development of these embryos, it was expected that these eggs would mature and hatch within a month after collection, since benthic egg masses of many northeast Pacific fishes mature to hatching within 1 to 3 mo after fertilization (pers. obs. on 28 species). The *T. trichodon* eggs, however, continued to develop for over 8 mo after they were collected, then all hatched within a 24-h period.

As a basis for comparison, wolf-eel, *Anarrhichthys ocellatus*, eggs are large (ca. 5 mm in diameter) and have a relatively long incubation of 3 mo at 10°-12° C (pers. obs. on captive spawn). At 1 mo after fertilization (one-third of incubation period), *A. ocellatus* embryos reach a developmental state comparable with that of the *T. trichodon* at the time of the collection, with pigmented eyes on an embryo still many times smaller than the yolk sac. Assuming comparability in relative rates of development, a full incubation period of 12 mo could therefore be calculated for the *T. trichodon*. An incubation period of 1 yr would indicate February as the time of spawning, which coincides with the finding of a ripe female in February in the same area of Vancouver Island (Clemens and Wilby 1961).

About 90% of the hatch occurred within 4 h, in late afternoon, the remainder the next morning. The *T. trichodon* eggs had not been handled for 2 wk prior to hatching and no other fish eggs had hatched in the incubation tank for a week prior to this hatch, so it appears unlikely that this abrupt hatch was unnaturally stimulated. Only a few egg mortalities occurred during the incubation period in the laboratory; this low egg mortality, together with the occurrence of an abrupt and fully viable hatch, indicates that the observed incubation period was normal for this species, as an abnormal incubation should adversely affect viability. Although incubation periods of about 1 yr have been reported for an unrelated fish species, *Agonus cataphractus* (see Breder and Rosen 1966 for review), such prolonged incubation is evidently rare.

The larvae were reared in the laboratory from hatching through metamorphosis with no mortalities (maximum age 29 mo, 137 mm SL). Larvae hatched on 15 and 16 February 1977 at 14.5 mm SL (16 mm TL) and grew to 40-43 mm SL (45-50 mm TL) in 70 d, by which time the fish resembled small adults. Allometric growth in the deeping and lateral compression of the ventral body continued to about 50 mm SL, along with upturning of the jaw and development of fringed lips, as shall be discussed in the following section.

Immediately upon hatching the larvae swam to the water surface and began schooling at the surface in a two-dimensional array (one-fish deep). This neustonic schooling behavior shifted to a pattern of subsurface schooling (three-dimensional schools, usually within 10 cm of the surface) at about 48 h after hatching. At this time, feeding was first noted. By 72 h after hatching, about half the larvae had food in the guts within 4 h of the daily food introduction; about 80% had full guts after introduction of food on day 4 (96 h). Schooling behavior was characteristic of the entire period of larval development; these schooling tendencies decreased progressively during metamorphosis (from about 30 to 50 mm SL) and the juveniles did not show true schooling behavior in the confines of aquaria.

The larval *T. trichodon* were rapid swimmers. Alexander (1967) mentioned 10 body lengths/s as a maximum burst speed for teleosts of any size and 3-5 body lengths/s as a maximum sustained speed (maintained for at least several minutes). Although no effort was made to determine precisely the cruising speed of larval *T. trichodon*, observations of the distance traversed in 5 s intervals revealed a cruising speed of about 10 body lengths/s and always over 5 body lengths/s. This rapid swimming occurred abruptly upon hatching, before the onset of feeding. Synchronized hatching, the abrupt onset of schooling, and rapid swimming may have evolved as mechanisms for larvae to escape the physical dangers of the wave-swept incubation site.

Trichodon trichodon first burrowed into sand as metamorphosed juveniles of 50-60 mm SL. They burrowed by simultaneously undulating the body laterally while fanning the pectoral fins upward and forward, so that the body sank downward and backward into the sand. The eyes and nostrils usually remained exposed above the sand, although the entire body could be buried. Burrowing did not occur until fleshy fringes had developed on the jaws. The fringed lips may permit water to be inhaled without allowing sand to enter the buccal cavity. The allometric growth prior to inital bur-

rowing may indicate a functional role of the deep, narrow form of the ventral part of the body in burrowing.

Larval Development

Morphometric and meristic features of an excised embryo (2 wk prior to hatching) and larvae of nine posthatching ages are presented in Table 1. The outstanding feature of the late embryo was the presence of caudal fin rays and a flexing notocord with the posterior margins of the hypural plates about 45° to the horizontal body axis. This precocious development of the caudal fin remained a diagnostic character throughout the larval period and probably contributed to the rapid swimming speeds discussed earlier.

The late embryo and the newly hatched larvae have a large oil droplet positioned anteriorly in the yolk. The abdomen has about 40 melanophores radiating from the dorsal gut surface. In addition to the features detailed in Table 1, these early ages have a few external melanophores in the nasal region, lower jaw angle, cranial region (7-10), and anterior mandibles (Figure 1). There is also an internal melanophore anterior to each otic capsule and, in fresh material, about 30 xanthophores over the cranium. Three preopercular spines are present as are the pectoral fin rays.

By 9 d hatching age, the posterior margins of the hypural plates are approaching a vertical orientation and have an increased number of melanophores, while the caudal and pectoral fin rays have increased in length. There is a row of 4 or 5 small melanophores along each side of the anterior insertion of the dorsal fin fold and an internal row of about 24 melanophores along the notocord (less clearly visible than external pigment, therefore not illustrated). Eight small melanophores have appeared in the cranial region, clustered among six larger ones, previously developed. A single melanophore has appeared on the ventral midline of the lower jaw (not visible in side view). Rows of melanophores have also appeared along the anterior end of the mandibles and horizontally on the dorsal portion of the operculum. Snout melanophores become prominent by this stage, as do teeth on the lower jaw. These teeth are easily visible at this stage, becoming progressively reduced until, at 25 d hatching age, they are no longer noticeable.

The 18-d specimen has vertical posterior margins on the hypural plates, a forked caudal fin, and

TABLE 1.—Count and morphometric data during early development of *Trichodon trichodon*. Fresh length, immediately after killing; preserved length, 1 yr later.

Hatched age (d)	Fresh length (mm SL)	Preserved length (mm SL)	SL, percent shrinkage	Preserved snout-anus length (mm)	Ratio snout-anus ÷ SL	Preserved body depth (mm)	Ratio body depth ÷ SL	Myomeres		Fin ray counts				Melanophore count	
								Preanal	Postanal	D-1	D-2	Anal	Pectoral	Pelvic	PVM[1]	Hypural
Embryo	—	11.0	—	—	—	—	—	12	36	0	0	0	—	0	16	3
0	14.5	13.0	10.3	4.5	0.35	2.5	0.19	12	38	0	0	0	—	0	18	3
0	14.5	13.0	10.3	4.5	0.35	2.7	0.21	12	38	0	0	0	—	0	16	1
0	14.5	13.0	10.3	4.5	0.35	2.7	0.21	12	40	0	0	0	—	0	20	2
9	—	14.5	—	5.0	0.34	3.0	0.21	12	37	0	0	0	—	0	16	4
18	19.5	17.2	11.8	7.0	0.41	3.3	0.19	12	37	0	0	0	21	0	20	6
25	21.0	20.0	4.8	8.7	0.43	4.2	0.21	14	34	VIII	15	28	21	0	18	Bands
29	24.5	22.0	6.1	9.3	0.42	5.0	0.23	15	34	X	19	27	21	0	[2]19 + 19	Bands
35	27.5	27.0	1.8	12.0	0.44	5.5	0.20	14	32	XII	18	1,28	21	3	19 + 21	Bands
43	29.0	28.0	3.4	12.7	0.45	6.8	0.24	15	34	XIII	18	1,28	21	1,3	25	Brackets
56	31.5	30.0	4.8	14.0	0.47	7.0	0.23	13	35	XIV	19	1,29	23	1,5	19	Brackets
56	32.5	32.0	1.5	15.0	0.47	7.0	0.22	14	36	XIII	18	1,28	21	1,5	20	Brackets
70	40.0	38.0	5.0	18.0	0.47	9.3	0.24	14	36	XIV	1,19	1,29	22	1,5	15	Brackets
70	43.0	40.5	5.8	20.5	0.51	11.0	0.27	14	34	XIV	1,17	1,27	22	1,5	12	Brackets

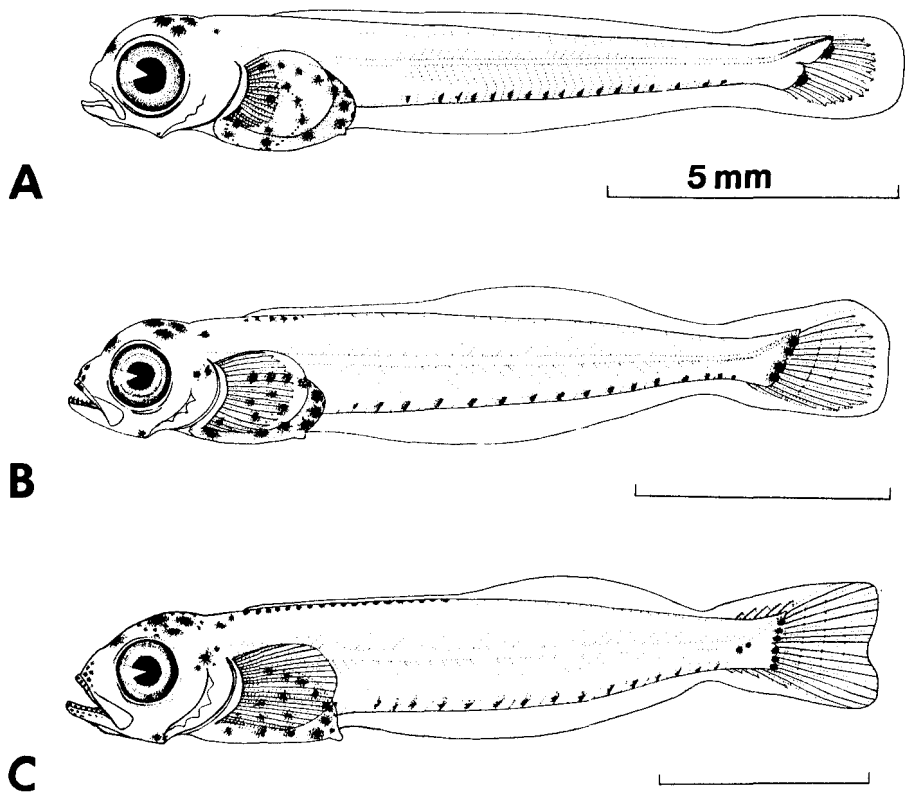
[1]Postanal ventral midline melanophores versus hypural melanophores.
[2]Internal and superficial melanophore counts.

secondary caudal fin rays. Melanophores are more numerous along the insertion of the dorsal fin fold (18-19 each side), internally along the notocord (27; vague, not illustrated), along the ventral midline of the lower jaw (10), in the cranial region (7 large, 23 small), and on the posterior margin of the hypurals (6). Melanophores appear larger and more dense on the dorsal gut surface as well. Two melanophores are present laterally at the angle of the notocord and 10 melanophores are visible on the principal caudal rays. Pectoral fin ray development is complete (21 rays) and four preopercular spines are evident.

By 25 d hatching age the melanic pigmentation of the dorsal body surface, jaw, and snout has proliferated considerably, while dorsal and anal fin ray development has started (Table 1) and pelvic fin buds are visible. Paired rows of 38 large melanophores occur on the dorsal body along the entire length of the dorsal fin. Cranial melanophores appear as a pair of dense patches (one on each side) with a third median patch on the nape region. The postanal ventral midline melanophores appear more internal than at younger ages. A new row of superficial melanophores has appeared on the mediolateral trunk musculature (posterior half of body), while the angle of the notocord is overlaid by an angular "bracket" of small melanophores, the dorsal leg of which continues anteriorly as a faint internal row dorsal to the notocord. The melanophores at the posterior margin of the hypurals form continuous vertical bands on each plate. Finally, a fifth preopercular spine is becoming visible ventrally.

The 29-d specimen (not illustrated in Figure 1) is marked by the appearance of a ring of small melanophores around each eye, the development of both internal and superficial ventral midline melanophores (Table 1) and doubled rows of melanophores along each side of the dorsal fin base on the anterior half of the body. Cranial and dorsal gut melanophores have continued to become more dense and the pelvic fins are formed, without elements.

At 35 d hatching age, melanophores are on the dorsal margin and dorsal insertion of the pectoral fin and melanophores are arrayed in double or triple rows on each side of the dorsal fin bases



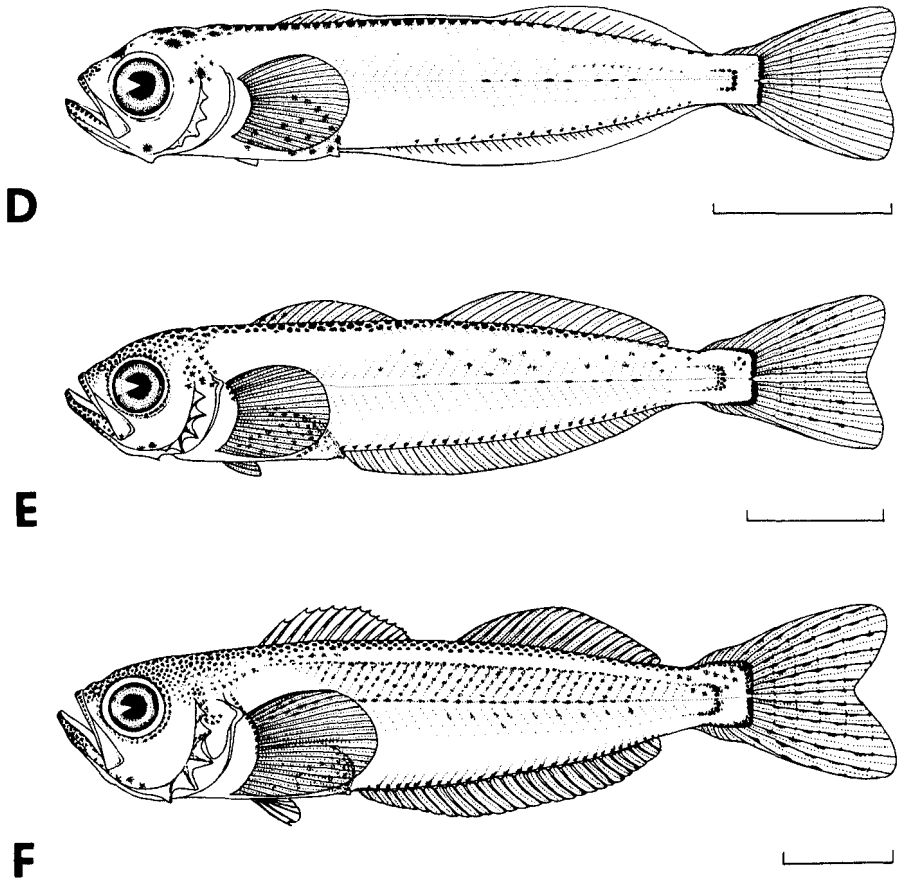


FIGURE 1.—Larvae and early juveniles of *Trichodon trichodon* (preserved lengths). A. 0 d, 13 mm SL; B. 9 d, 14.5 mm SL; C. 18 d, 17.2 mm SL; D. 25 d, 20 mm SL; E. 35 d, 27 mm SL; F. 56 d, 32 mm SL.

posteriorly to the middle of the second dorsal, continuing as single rows across the peduncle. Melanophores are on the first three elements of the first dorsal fin. On the lower jaw, melanin has extended posteriorly to the juncture with the maxillaries. A patch of melanophores has developed on the dorsal preoperculum. About 26 scattered melanophores appear dorsolaterally on the trunk musculature, above the mediolateral row, and melanophores occur closely spaced, lining the edges of principal caudal rays. The melanophores on the hypural margins have spread anteriorly along the insertion of the secondary caudal rays. Allometric growth at this age includes an increase in the relative snout-anus length (Table 1) and a slight upturning of the jaw.

The 43-d specimen (not illustrated) exhibits more regular arrays of the most recently developed melanophore patterns: the mediolateral row consists of 33 melanophores, the dorsolateral melanophores now form broken rows along the margins of myomeres, and the caudal rays are lined with rows of melanophores. By this age, gut melanophores appear internal rather than external. Only superficial ventral midline melanophores (25) are visible.

The 56-d specimen is easily recognized as a young sandfish. The entire snout, jaw, cranium, and nape regions are densely covered with melanophores, continuous with rows along the dorsal fin bases. The upper pectoral fin rays are lined with melanophores, as are the spines on the anterior half of the first dorsal fin. More melanophores have appeared over the caudal peduncle. All fins are completely formed by this stage and the five preopercular spines appear to radiate from a centrum.

By 70 d hatching age the body proportions re-

semble those of the adult. Hart (1973) listed body depth as 0.28 SL for adults, which compares with 0.27 SL for the 70-d specimen (Table 1). The snout-anus length has reached the adult proportion of 0.5 SL (Hart 1973) by this stage. The jaw angle and eye position have not attained adult character by 70 d, however, and the fringed lips and elongate nostrils of the adult are not evident. These features are present by the time burrowing behavior first appears at sizes of about 55-60 mm SL (165 d).

Discussion

Larvae of *T. trichodon* are distinct and easily identified. Myomere counts alone would separate *T. trichodon* from other elongate larvae in the northeastern Pacific. As mentioned, the early development of the caudal fin is a distinguishing character of all early larval stages of *T. trichodon*. The newly hatched yolk-sac larva has a flexed notocord and developing caudal rays. The caudal fin is forked and has secondary rays developing prior to the development of elements of other median fins.

The melanophore patterns developed in gradual stages with little variation among the individuals from this particular hatch. The most distinctive melanophores are perhaps those in the caudal region, on the hypural margins, and at the notocord bend. The overall melanophore patterns for each stage could probably be used as a basis for diagnosis, certainly when taken together with the morphometry and fin development patterns.

The preopercular spines are present at hatching and seem unique among sympatric elongate larvae. The stellate arrangement of these spines in the later development stages is unique.

Altogether, there appears to be little chance for misidentification of this species in the northeast Pacific region. This is of interest in light of the absence of these larvae from records of ichthyoplankton surveys in this region (e.g., Richardson and Pearcy 1977). In the Gulf of Alaska, where *T. trichodon* is an abundant inshore fish species, only one larva has been taken by plankton nets in an extensive ichthyoplankton survey (Kendall[2]). The only other northeast Pacific larvae, of which I am aware, with such high-speed schooling in a laboratory situation are those of *Ascelichthys rhodorus* (pers. obs.), which also do not appear in plankton nets (Richardson and Pearcy 1977). Although this behavior may enhance evasive capabilities in areas sampled for plankton, a further possibility is that this behavior may enable larvae to inhabit the extreme nearshore, which is usually not included in regular plankton surveys.

[2]Arthur W. Kendall, Jr., Fishery Biologist, Northwest and Alaska Fisheries Center, NMFS, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112, pers. commun. August 1979.

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JEFFREY B. MARLIAVE

Vancouver Public Aquarium
P.O. Box 3232
Vancouver, B.C. V6B 3X8 Canada